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On the diagnostic characters of the genus *Stygonitocrella* (Copepoda, Harpacticoida), with descriptions of seven new species from Australian subterranean waters

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Abstract

Seven new freshwater ameirids were discovered in the Australian subterranean habitats, six of which would fit into the present unsatisfactory diagnosis of the genus *Stygonitocrella* Reid, Hunt & Stanley, 2003. Two of them were discovered in Pioneer Valley, Queensland, representing the first record of this genus in eastern Australia. Four other species were collected from the Pilbara region in Western Australia, the same region in Australia where the first three representatives of this genus were reported. An additional new species was collected in the Kimberley region in Western Australia and could not be assigned to the revised genus *Stygonitocrella*, but has some remarkable similarities with species that were in the past considered to be members of this genus. In order to assess the most natural allocation of these ameirid taxa, a revision of the genus *Stygonitocrella* was made, based on a cladistic approach by using 57 phylogenetically informative morphological characters. The phylogenetic analysis revealed the presence of six monophyletic groups, giving ground for the establishment of six new genera, three of them created to accommodate a single new Australian species: *Kimberleynitocrella billhumphreysi* **gen. et sp. nov.** from several bores in the Argyle Diamond Mine and Ord River in the Kimberley region in Western Australia, *Gordanitocrella trajani* **gen. et sp. nov.** from three different localities in the Pilbara region in Western Australia, and *Lucionitocrella yalleenensis* **gen. et sp. nov.** from a single bore on the Yalleen Station, also in the Pilbara region in Western Australia. All three new Australian genera have a basal position on the phylogenetic tree, because they share several plesiomorphic characters; nevertheless they are well defined by the combination of apomorphic and plesiomorphic features. The generic diagnosis of *Stygonitocrella* is emended and the genus redefined to include only four species: *S. montana* (Noodt, 1965) from Argentina (the type species), *S. dubia* (Chappuis, 1937) and *S. guadalfensis* Rouch, 1985 from Spain and *S. sequoyahi* Reid, Hunt & Stanley, 2003 from the United States. The Cuban *S. orghidani* (Petkovski, 1973) was left as *incertae sedis* in this genus. The subgenus *Fiersiella* Huys, 2009 is established as a junior subjective synonym of *Stygonitocrella*. Generic diagnoses are emended for the monospecific Australian genus *Inermipes* Lee & Huys, 2002, the monospecific Japanese genus *Neonitocrella* Lee & Huys, 2002 and the North American genus *Psammonitocrella* Huys, 2009, that contains two species. The genus *Reidnitocrella* **gen. nov.** is erected to accommodate three closely related central Asian species: *R. tianschanica* (Borutzky, 1972) comb. nov., *R. pseudotianschanica* (Sterba, 1973) comb. nov., and *R. djirgalanica* (Borutzky, 1978) comb. nov. Also, after carefully examining the available published information on *R. tianschanica* another new species is recognized in this genus: *R. borutzkyi* **sp. nov.** The genus *Eduardonitocrella* **gen. nov.** is erected for the Mexican *E. mexicana* (Suárez-Morales & Iliffe, 2005) comb. nov. The newly established genus *Megastygonitocrella* **gen. nov.** is the largest one in this group of freshwater ameirids, containing the following 11 species: *M. trispinosa* (Karanovic, 2006) comb. nov. (type species), *M. bispinosa* (Karanovic, 2006) comb. nov., *M. unispinosa* (Karanovic, 2006) comb. nov., *M. ecowisei* **sp. nov.**, *M. dec* **sp. nov.**, *M. pagusregalis* **sp. nov.**, *M. kryptos* **sp. nov.**, *M. karamani* (Petkovski, 1959) comb. nov., *M. petkovskii* (Pesce, 1985) comb. nov., *M. ljovuschkini* (Borutzky, 1967) comb. nov. and *M. colchica* (Borutzky & Michailova-Neikova, 1970) comb. nov. The first five species are endemic to the Pilbara region in Western Australia, the next two are described from Queensland, *M. karamani* is known from Slovenia, *M. petkovskii* from Greece, while the last two species are endemic to the Caucasus. A Tethyan origin for this genus is here hypothesized. New locality data is presented for the first three species, which revealed that *M. trispinosa* is the most common and widely distributed member of this group (although restricted to a single Australian region), while *M. bispinosa* and *M. unispinosa* are short range endemics. A key to species is provided for each polytypic genus, as well as a key to genera of *Stygonitocrella s. l.*

Key words: Stygofauna, taxonomy, systematics, cladistics, revision, freshwater, Ameiridae

Introduction

In *Stygofauna Mundi* (Botosaneanu 1986), an important reference work for subterranean biologists, Europe was divided into 34 different regions and subregions (actually zones, provinces and districts in the original terminology) and the Balkan Peninsula alone into no less than 13. Although of a comparable size, the Australian continent was only divided zoogeographically into Western Australia and "Other areas of Australia (including Tasmania)", without any maps or precise borders. This is not surprising considering the amount of knowledge available on Australian stygal organisms in 1986, where the only subterranean copepods known were four harpacticoid species from marine interstitial, all described by Nicholls (1945a, b). At that time arid zones were considered to have little potential for supporting specialized subterranean faunas, owing to the lack of water and low nutrient input from xeric plant communities (Peck 1978; Howarth 1980), and this misconception has also been extended to the Australian continent (Moore 1964; Hamilton-Smith 1967; Barr 1973). Thus the groundwater fauna here remained little studied and apart from some early descriptions of fish and decapods (e.g. Whitely 1945; Holthuis 1960), information was mostly restricted to caves (Humphreys & Adams 1991; Poore & Humphreys 1992; Thurgate *et al.* 2001a, b). The pioneering work of Dr William F. Humphreys in the Western Australian calcrete and limestone systems offered a new perception of groundwater ecosystems in arid Western Australia, where ground water were found to harbour unique subterranean faunas (Humphreys 2001, 2006, 2008).

During the last decade many subterranean copepods have been described from Australian freshwater (Pesce *et al.* 1996a, b; Pesce & De Laurentiis 1996; De Laurentiis *et al.* 1999, 2001; Karanovic 2003, 2004a, b, 2005, 2006; Tang *et al*. 2008; Tang & Knott 2009), anchialine (Karanovic *et al.* 2001; Karanovic & Pesce 2002; Karanovic & Eberhard 2009) and marine interstitial habitats (Karanovic 2008), and many more species await description.

Karanovic (2006) described three new species of the genus *Stygonitocrella* Reid, Hunt & Stanley, 2003 as the first representatives of this freshwater ameirid group from Australia. Specimens were collected during the large Pilbara regional survey, led by the Western Australian Department of Conservation and Land Management (now the Department of Environment and Conservation), motivated by the need to assess the likely environmental impacts of economically important natural resources development projects (mostly mining) on stygofauna. In Western Australia it is necessary for any new development that potentially impacts on groundwater to be preceded by biological surveys of groundwater biodiversity. In the subsequent years, many private environmental consulting agencies, as well as individuals from several academic institutions, continued to collect stygofauna in Australia and most of the copepod material collected was entrusted to the senior author for identification. Here we describe seven new species that would fall into the original diagnosis of *Stygonitocrella* as defined by Petkovski (1976) (*Stygonitocrella s. l.* in this paper) from two regions in Western Australia (Pilbara and Kimberley) and one small area in Queensland.

The genus name *Stygonitocrella* was established by Petkovski (1976) in an attempt to revise the genus *Nitocrella* Chappuis, 1924. The latter was established by Chappuis (1924) to accommodate a new species from Serbia, *Nitocrella hirta* Chappuis, 1924, but in subsequent years many authors (including Chappuis himself) have used the genus as a taxonomic repository, which blurred its boundaries in a remarkable way. Even after Lang's (1965) revised taxonomic concept, *Nitocrella* continued to accumulate a large number of not very closely related new species, which prompted Petkovski (1976) to subdivide the genus even further. He defined *Stygonitocrella* for those species of *Nitocrella* with the endopod of the fourth leg one-segmented and the endopods of the second and thid legs one- or two-segemented, i.e. with the segmentation formula of 2.2.1, 2.1.1 or 1.1.1. He also compiled a key to the following nine species recognized by him as valid at the time: *Stygonitocrella dubia* (Chappuis, 1937) described from Spain by Chappuis (1937); *S. karamani* (Petkovski, 1959) from Macedonia (Petkovski 1959); *S. montana* (Noodt, 1965) from Argentina (Noodt 1965); *S. ljovuschkini* (Borutzky, 1967) from the Russian NW part of the Caucasus (Borutzky 1967); *S. colchica* (Borutzky & Mihailova-Neikova, 1970) from Gruzia (Borutzky & Mihailova-Neikova 1970); *S. tianschanica* (Borutzky, 1972) from Kyrgyzstan (Borutzky 1972); *S. insularis* (Miura, 1962) from Japan

(Miura 1962); *S. pseudotianschanica* (Sterba, 1973) from Afghanistan (Sterba 1973); and *S. orghidani* (Petkovski, 1973) from Cuba (Petkovski 1973). Note that Petkovski (1976) misspelled the names of *S. tianschanica* and *S. pseudotianschanica* as *"tianshanica"* and *"pseudotianshanica"*. He also did not designate a type species, which according to the current International Code of Zoological Nomenclature (ICZN 1999, Article 13.3) means that the generic name was unavailable. In order to be available every new genus-group name published after 1930 must be accompanied by the fixation of a type species, in addition to satisfying the provisions of Article 13.1, i.e. providing or citing a description or definition of the genus.

Nevertheless, new species of this genus have been subsequently described, such as *S. petkovskii* Pesce, 1985 from Greece (Pesce 1985) and *S. guadalfensis* Rouch, 1985 from Spain (Rouch 1985), and it was clear that Borutzky (1978) was not aware of Petkovski's (1976) paper when describing *Nitocrella djirgalanica* Borutzky, 1978 from Kyrgyzstan, as it represents another member of *Stygonitocrella*.

Later on Rouch (1992) described two new species from the United States in a newly erected genus *Psammonitocrella* Rouch, 1992, although both species (*P. boultoni* Rouch, 1992 and *P. longifurcata* Rouch, 1992) would have fitted nicely into the original diagnosis of the genus *Stygonitocrella* as defined by Petkovski (1976). However without the mandatory type fixation, the generic name was unavailable until Huys (2009) fixed *P. boultoni* as the type species, making the name available under his authorship. Rouch (1992) recognized a number of well defined autapomorphic charater states for the new genus and his two closely related species provided evidence that the segmentation of the endopodal segments of the second and third legs can be reduced from a two-segmented stage into a one-segmented stage in a single evolutionary event. Lee & Huys (2002) used this knowledge to separate *S. insularis* into a new monospecific genus *Neonitocrella* Lee & Huys, 2002. They also described one new species from Western Australia in a newly erected genus *Inermipes* Lee & Huys, 2002 (*I. humphreysi* Lee & Huys, 2002). They commented on the "artificial" status of *Stygonitocrella* (sometimes even using the term "unnatural genus", probably meaning polyphyletic) and compared the swimming legs setal formulae of 13 species, recognizing "the presence of several discrete lineages within the genus". However, they refrained from giving any additional information about these "lineages" or naming them, stating that the "formal recognition of these lineages as distinct genera is impossible since most descriptions are severely lacking in detail".

Finally, Reid *et al.* (2003) designated *S. montana* as the type species of the genus and gave a revised diagnosis, making the generic name available with their authorship, i.e. *Stygonitocrella* Reid, Hunt & Stanley, 2003. This was accepted by Lee & Huys (2002), Karanovic (2006) and Wells (2007), although Suárez-Morales & Iliffe (2005) continued to attribute the authorship to Petkovski (1976). Note that the paper of Reid *et al.* (2003) was published later than that of Lee & Huys (2002), but the latter authors had access to an unpublished manuscript of the former authors. Reid *et al.* (2003) also described a new species, *S. sequoyahi* Reid, Hunt & Stanley, 2003, as the first *Stygonitocrella* representative from North America. On the same occasion they treated all previously described species as new combinations and cited all author names in parentheses. Although neither Article 11.9.3 nor Article 51.3 of the ICZN specifically addresses this case, this was not a case of a generic name being different from the original one, since the author attribution does not form part of a name in zoological nomenclature (Article 51.1). Therefore, we think parentheses should not have been used and it was at least an overstatement to refer to such cases as new combinations. Suárez-Morales & Iliffe (2005) described a new species from Mexico and proposed a subdivision of *Stygonitocrella* into two subgenera, *Eustygonitocrella* Suárez-Morales & Iliffe, 2005 and *Fiersiella* Suárez-Morales & Iliffe, 2005, based on the condition of the female fifth leg baseoendopod. We will show in this paper that their subdivision of the genus is not taxonomically sound, but it also suffers from some serious nomenclatural problems. As Wells (2007) pointed out, *Eustygonitocrella* is obviously an objective synonym of *Stygonitocrella,* since it contains the type species *S. montana*, and must, therefore, be relegated to a junior synonym of the nominotypical subgenus (ICZN Article 44.1). For the subgenus *Fiersiella* the authors designated *Stygonitocrella dubia* as "... the representative species ...", without following the rules of the ICZN (Article 67.5), making this genus-group name unavailable. According to the provisions of the Code, type designation must be rigidly constructed by using the term "type species" (or an equivalent term in another

language) to avoid ambiguity. Huys (2009) made the subgeneric name available by fixing *S. sequoyahi* as the type species. Unfortunately, our study shows that both *S. dubia* and *S. sequoyahi* belong to the same clade as the type species of *Stygonitocrella*, and as such, *Fiersiella* Huys, 2009 is regarded here as a subjective junior synonym of the former. The Mexican *Stygonitocrella mexicana* Suárez-Morales & Iliffe, 2005 is in this paper transferred into a newly described monospecific genus.

Being that the systematics of the family is still in flux, and considering the great variation observed in body plans among the species analysed, we felt it timely to review the taxonomic status of the genus *Stygonitocrella* in order to find the more natural allocation of these taxa. The revision was carried out by performing a cladistic analysis based on 57 morphological characters. This is the first attempt to revise this branch of a family that is notorious for its ill-defined genera and where the fine-level systematics is considered problematic by many taxonomists (Conroy-Dalton & Huys 1997, 1998; Lee & Huys 2002; Reid *et al.* 2003; Karanovic 2006). The primary taxonomic subdivisions in freshwater ameirids have been traditionally based on swimming leg segmentation (Lang 1948, 1965; Petkovski 1976), an approach characterised as simplistic and creating many "unnatural" genera by Lee & Huys (2002), Reid *et al.* (2003) and Karanovic (2006), although none of them provided an alternative solution. The revision based on the cladistic analysis resulted in description of six new genera (three based on freshly collected material) and eight new species (seven from new material).

Material and methods

Most specimens studied here were collected by private environmental consulting agencies (Outback Ecology, Ecowise Australia, Subterranean Ecology) and sent for identification to the senior author. They resulted from various impact assessment and monitoring projects, primarily done for the mining industry. Some specimens were collected during the Pilbara regional survey, led by the Western Australian Department of Environment and Conservation (DEC), and some were sent for identification by the Western Australian Museum (WAM). Material from Queensland was collected during a research project of the junior author. In total 118 samples were studied from around 85 different localities (some of them very close to each other) in the Pilbara and Kimberley regions in Western Australia and Pioneer Valley in Queensland. Locality data and number of specimens are listed for every species separately and most of the material is deposited in the Western Australian Museum, Perth, except some voucher specimens of previously decribed species are kept in the Department of Environment and Conservation.

Samples were collected with haul-nets (mesh size 50, 150, 250 or 350 µm) or a groundwater sampling pump from bores and wells. Bores are holes mainly drilled by mining companies or agricultural enterprises for the purpose of water monitoring and abstraction or mineral exploration. They are usually 10 to 20 cm in diameter and may be lined entirely, or in part, by PVC tubing (the casing). This tubing may be open only at the bottom, or it may be pierced at one or more levels by holes of various sizes ("slots"). The top may be securely capped or entirely open to the elements. Some bores record water pressure at a given level in the aquifer (piezometers), while others, together with hand dug wells (ca. 1 × 1.5 m) equipped with windmills, provide water for pastoral use. Many of these features are derelict. Haul-nets are actually simple plankton nets of a different size suitable for the bore; collar can range from 30 to 200 mm in diameter and is made of stainless steel. Weighed nets (using simple fishing leads, or more complicated brass intermediate collars) were lowered down into the bore with a bottle screwed on its distal part and then hauled through the water column, usually a number of times. A Waterra groundwater sampling pump was used to collect 300 litres of water, which was then filtered through a plankton net. The Bou-Rouch pump and Karaman-Chappuis methods were used for sampling stygofauna from the interstitial habitats (mostly near permanent springs). Samples were sorted live under a dissecting microscope and copepods picked out and fixed in 70% or 100% ethanol and assigned a field number (Prefix BES for the Museum samples, but every consulting agency has a different system of numbering its samples), or were preserved in the field in 100% ethanol and sorted in a laboratory. Many bores

established for hydrogeological work, mineral exploration and water monitoring have prefixes or suffixes of relevance only to that drilling program. These codes are cited in the material examined for each species to aid specification of the location, although precise coordinates are also provided for each sample.

Specimens were dissected and mounted on microscope slides in Faure's medium, which was prepared following the procedure discussed by Stock & von Vaupel Klein (1996), and dissected appendages were then covered by a coverslip. For the urosome or the entire animal two human hairs were mounted between the slide and coverslip, so the parts would not be compressed. By manipulating the coverslip carefully by hand, the whole animal or a particular appendage could be positioned in different aspects, making possible the observation of morphological details. During the examination water slowly evaporated and appendages eventually remained in a completely dry Faure's medium, ready for long term depositing. All drawings were prepared using a drawing tube attached to a Leica-DMLS brighfield compound microscope, with C-PLAN achromatic objectives. Specimens that were not drawn were examined in a mixture of equal parts distilled water and glycerol and, after examination, were again preserved in 70% ethanol.

Morphological terminology follows Huys & Boxshall (1991), except for caudal ramus setae numbering and small differences in the spelling of some appendages (antennula, mandibula, maxillula instead of antennule, mandible, maxillule), as an attempt to standardise the terminology for homologous appendages in different crustacean groups. Also, for the armature formula of the swimming legs a much simplified version is used. The only reason for this is that there are a number of transitional forms between spine and seta in copepods. To avoid possible confusion in some descriptions we sometimes use the term "armature element" (or just "element") instead of spine or seta. Biospeleological terminology follows Humphreys (2000).

The cladistic analysis was performed on 28 species of *Stygonitocrella s. l.* from around the world. *Biameiropsis barrowensis* Karanovic, 2006 was chosen as the outgroup. This species was described from anchialine waters of Barrow Island (NW Western Australia) and it is among the most primitive members of the family Ameiridae Monard, 1927 (see Karanovic 2006). Many plesiomorphic features observed in *Stygonitocrella s. l.* species presented here, and especially in the species from the Kimberley region, prompted us to choose *B. barrowensis* and not some other freshwater ameirid with more reduced swimming legs. This species will probably also be a very suitable outgroup for any future cladistic analyses of other freshwater ameirid genera. It should be mentioned here that the species name was spelled incorrectly (as *B. barrowi*) in Karanovic (2006) in the figure legends and after the generic diagnosis, which was also used by Wells (2007). Accorging to the ICZN Article 24.2.3 “If a name is spelled in more than one way in the original work, the first author to have cited them together and to have selected one spelling as correct is the First Revisor”. Unfortunately Wells (2007) mentioned only *B. barrowi* and cannot be considered the First Revisor. Here, we select *B. barrowensis* and fix it as the correct original spelling, making *B. barrowi* incorrect and therefore unavailable (Article 32.4).

A total of 57 morphological characters were used in the analysis (Table 1). Characters were coded, optimized and weighted using the computer program WinClada, version 1.00.08 (Nixon 2002), and then analyzed using NONA, version 2 (Goloboff 1999). Standard coding was used in the analysis: "0" representing a presumably plesiomorphic character state and "1" a presumed apomorphy. Unknown character states were coded "-" and polymorphic characters are marked in the matrix with an asterisk (*). Characters of the fifth and sixth legs (47–56) were weighted 0.5 because of great variability in apparently closely related species; all other characters were weighted 1. All characters were coded as additive (representing ordered multistate character as a linked series of binary characters). A data matrix was created (Table 2) and characters analysed using the Rachet Island Hopper searches with the WinClada default parameters: 200 replications; 1 tree to hold; 3 characters to sample; 10 random constraint level and amb-poly= (amb- collapses a branch if the ancestor and descendant have different states under the same resolutions of multistate characters or of "-"; poly= treats trees as collapsed). Rachet is a method that searches tree space very effectively by reducing the search effort spent on generating new starting points and retaining more information from existing results of tree searches.

TABLE 1. Characters and character states used in the cladistic analysis of *Stygonitocrella s. l.*

No.	Character	State 0	State 1
0	Habitus in dorsal view	Unconstricted	Constricted at genital somite
1	Genital somite in female	Fused with first abdominal somite	Free
2	Lateral cuticular windows on third and fourth pedigerous somites	Present	Absent
3	Dorsal cuticular window on cephalothorax	Present	Absent
4	Caudal rami in proportion to anal somite	Shorter	Longer
5	Position of operculum on anal somite	Midlength	Posterior
6	Antennula, seta on first segment	Present	Absent
7	Antennal exopod, outer seta	Present	Absent
8	Antennal exopod, middle seta	Present	Absent
9	Mandibular basis, inner seta	Present	Absent
10	Maxillular endopod, dorsal apical seta	Present	Absent
11	Maxillular endopod, ventral apical seta	Present	Absent
12	Maxilla, proximal endite	Present	Absent
13	Maxillar endopod, dorsal apical seta	Present	Absent
14	Maxilliped, seta on syncoxa	Present	Absent
15	Maxilliped, small seta on endopod	Present	Absent
16	First and second leg basis, outer element	Present	Absent
17	First leg, second exopodal segment, inner element	Present	Absent
18	First leg, second exopodal segment, outer spine	Present	Absent
19	First leg, third exopodal segment, proximal outer spine	Present	Absent
20	First leg, first endopodal segment, inner seta	Present	Absent
21	First leg, inner spine on basis in male	Transformed	Similar to female
22	First leg, third endopodal segment, small inner seta	Present	Absent
23	Second leg, third exopodal segment, proximal outer spine	Present	Absent
24	Second leg, third exopodal segment, distal inner seta	Present	Absent
25	Second leg, ultimate endopodal segment, outer subapical spine	Present	Absent
26	Second leg, ultimate endopodal segment, outer apical seta	Present	Absent
27	Second leg, ultimate endopodal segment, inner apical seta	Present	Absent
28	Second leg, ultimate endopodal segment, distal inner element	Present	Absent
29	Second leg, ultimate endopodal segment, proximal inner seta	Present	Absent
30	Second leg, penultimate endopodal segment, inner seta	Present	Absent
31	Second leg, third exopodal segment, inner apical seta	Present	Absent
32	Third and fourth legs, third exopodal segment, middle outer spine	Present	Absent
33	Third and fourth legs, third exopodal segment, inner apical seta	Present	Absent
34	Third leg, third exopodal segment, middle inner seta	Present	Absent
35	Third leg, ultimate endopodal segment, outer subapical spine	Present	Absent
36	Third leg, ultimate endopodal segment, outer apical seta	Present	Absent
37	Third leg, ultimate endopodal segment, inner apical seta	Present	Absent
38	Third leg, ultimate endopodal segment, distal inner seta	Present	Absent

continued next page

TABLE 1. (continued)

No.	Character	State 0	State 1
39	Third leg, ultimate endopodal segment, middle inner element	Present	Absent
40	Third leg, penultimate endopodal segment, distal inner element	Present	Absent
41	Fourth leg, third exopodal segment, proximal inner seta	Present	Absent
42	Fourth leg, third exopodal segment, distal inner seta	Present	Absent
43	Fourth leg, ultimate endopodal segment, outer subapical spine	Present	Absent
44	Fourth leg, ultimate endopodal segment, outer apical seta	Present	Absent
45	Fourth leg, ultimate endopodal segment, inner apical seta	Present	Absent
46	Fourth leg, ultimate endopodal segment, distal inner seta	Present	Absent
47	Fifth leg exopod, innermost seta	Present	Absent
48	Fifth leg exopod, second seta from inner side	Present	Absent
49	Fifth leg exopod, third seta from inner side	Present	Absent
50	Fifth leg exopod, outermost (ancestral fifth) seta	Present	Absent
51	Fifth leg endopodal lobe, second element from outer side	Present	Absent
52	Fifth leg endopodal lobe, third element from outer side	Present	Absent
53	Fifth leg endopodal lobe, fourth element from outer side	Present	Absent
54	Male sixth leg, inner element	Present	Absent
55	Male sixth leg, middle element	Present	Absent
56	Male sixth leg, outer element	Present	Absent

TABLE 2. Character matrix for the phylogenetic analysis between species of *Stygonitocrella s. l.* Note that several species previously described or relocated to new genera as well as three of the seven new Australian species described herein are listed with their correct generic placement, while all others are presented as if belonging to the genus *Stygonitocrella* Reid, Hunt & Stanley, 2003.

Taxon	Characters
	1 2 3 4 5
	0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6
B. barrowensis	0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
K. billhumphreysi	0 0 1 1 0 1 0 0 0 1 1 1 1 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 * 1 0 0 0 0 0 0 1 0 * 1 0 0 1 1 1 1 0 0 0 0 1 1 1 1 1 0
G. trajani	0 0 1 1 0 1 0 1 0 1 1 0 1 0 0 0 0 0 0 0 0 0 0 1 0 1 0 1 0 1 1 0 0 0 0 1 0 1 0 0 1 1 0 1 0 1 1 0 0 1 0 1 1 1 1 0 0
L. yalleenensis	0 0 1 1 0 1 0 1 1 1 1 0 1 0 0 0 0 0 0 1 0 0 0 0 1 1 0 1 0 1 1 0 0 0 1 1 0 0 1 0 1 1 0 1 0 1 0 0 0 0 1 1 1 1 1 1 1
N. insularis	0 1 1 1 0 1 0 1 0 1 - - 1 1 - - 0 1 0 1 0 0 1 1 1 0 0 1 1 1 1 0 0 0 1 0 0 1 1 1 1 1 0 1 1 1 1 0 0 1 1 1 1 1 - - -
P. boultoni	0 1 1 1 1 1 1 0 0 1 1 1 1 1 1 1 1 0 1 1 1 1 1 1 1 1 0 1 1 1 1 1 1 1 1 1 0 1 1 1 1 1 0 1 1 1 1 0 0 1 0 1 0 1 - - -
P. longifurcata	0 1 1 1 1 1 1 0 0 1 0 0 1 1 1 1 1 0 1 1 1 1 1 1 1 1 0 1 1 1 1 1 1 1 1 1 0 1 1 1 1 1 1 1 1 1 1 0 * 1 * 1 1 1 - - -
I. humphreysi	1 0 1 1 0 1 1 1 1 1 1 1 1 0 1 1 1 1 0 1 0 0 1 1 1 0 1 1 1 1 1 0 0 0 1 0 0 1 1 1 1 1 0 0 1 1 1 0 1 1 1 1 1 1 1 1 1
S. bispinosa	0 0 1 0 0 1 0 0 0 1 1 0 1 0 0 0 0 1 0 1 0 0 0 1 1 0 1 1 1 1 1 0 0 0 1 0 0 1 1 1 1 0 0 0 1 1 1 0 0 0 0 0 1 0 1 * 0
S. borutzkyi	0 0 1 1 0 1 0 0 0 1 - - - - - - 0 0 0 1 0 0 0 1 1 0 0 1 1 1 0 0 0 0 1 0 0 1 1 1 * 0 0 0 1 1 1 0 0 0 1 1 1 1 1 1 1
S. colchica	0 - 1 1 0 1 - 0 0 - - - - - - - 0 1 0 1 0 0 0 1 1 0 1 1 1 1 1 0 0 0 1 0 0 1 1 1 1 1 0 0 1 1 1 0 0 0 0 0 0 0 - - -
S. dec	1 1 1 1 0 1 0 1 0 1 1 0 1 0 0 0 0 1 0 1 0 0 0 1 1 0 1 1 1 1 1 0 0 0 1 0 0 1 1 1 1 1 * 0 1 1 1 0 0 0 0 1 1 1 1 0 0
S. djirgalanica	0 - 1 1 0 1 - 0 0 - - - - - - - 0 0 0 1 - 0 0 1 1 0 0 1 1 1 1 0 0 0 1 0 1 1 1 1 1 0 0 0 1 1 1 1 1 1 1 1 1 1 - - -
S. dubia	0 - 1 1 0 1 - 0 0 - - - - - - - 0 0 0 1 1 0 0 1 1 1 0 1 1 1 1 0 0 0 1 1 0 1 1 1 1 0 0 1 0 1 1 0 0 1 0 0 0 0 1 0 0
S. ecowisei	0 0 1 1 0 1 0 0 0 1 1 0 1 0 0 0 0 1 0 1 0 0 0 1 1 0 1 1 1 1 1 0 0 0 1 0 0 1 1 1 1 1 0 0 1 1 1 0 0 0 0 0 0 1 1 0 0
S. guadalfensis	0 0 1 1 0 1 0 0 0 0 1 0 0 0 0 1 0 1 0 1 1 0 1 1 1 1 0 1 1 1 1 0 0 0 1 1 0 1 1 1 1 0 0 1 0 1 1 0 0 0 0 1 1 1 - - -
S. karamani	0 1 1 1 0 1 0 0 0 0 - - - - - - 0 1 0 1 0 0 0 1 1 0 0 1 1 1 1 0 0 0 1 0 0 1 1 1 1 1 1 0 1 1 1 0 0 0 0 0 1 0 * 0 0
S. kryptos	0 - 1 1 0 1 0 0 0 1 1 0 1 0 0 0 0 1 0 1 0 0 0 1 1 0 1 1 1 1 1 0 0 0 1 0 0 1 1 1 1 1 0 0 1 1 1 1 0 0 0 1 1 1 0 1 0
S. ljovuschkini	0 0 1 1 0 1 - 0 0 - - - - - - - 0 1 0 1 0 0 0 1 1 0 1 1 1 1 1 0 0 0 1 0 0 1 1 1 1 1 1 0 1 1 1 0 0 0 0 0 0 0 1 0 0
S. mexicana	0 1 1 1 0 0 1 1 0 1 1 0 1 1 1 1 0 1 0 0 1 - 0 1 1 1 0 0 1 1 1 0 0 0 1 1 0 0 0 1 1 1 1 0 0 1 0 0 0 1 1 1 1 1 - - -
S. montana	0 1 1 1 0 1 - 0 0 1 1 1 0 - - - 0 0 0 1 0 0 0 1 1 1 0 1 1 1 1 0 0 0 1 1 0 1 1 1 1 1 0 1 0 1 1 0 0 0 1 1 1 1 1 0 0
S. orghidani	0 - 1 1 0 1 - 1 0 - - - - - - - 0 1 0 1 0 0 1 1 0 1 0 1 1 1 1 0 0 0 0 1 0 1 1 1 1 1 0 1 0 1 1 1 1 1 1 1 1 1 - - -
S. pagusregalis	0 1 1 1 0 1 0 0 0 1 1 0 1 0 0 0 0 1 0 1 0 - 0 1 1 0 1 1 1 1 1 0 0 0 1 0 0 1 1 1 1 1 1 0 1 1 1 1 0 0 0 1 1 1 - - -
S. petkovskii	0 1 1 1 0 1 - 0 0 - - - - - - - 0 1 0 1 0 - 0 1 1 0 1 1 1 1 1 0 0 0 1 0 0 1 1 1 1 1 1 0 1 1 1 0 0 0 0 0 0 1 - - -
S. pseudotianschanica	0 0 1 1 0 1 - 0 0 1 - - - - - - 0 0 0 1 0 - 0 1 1 1 0 1 0 1 0 0 0 0 1 0 0 1 1 1 1 0 0 0 1 1 1 0 0 1 1 1 1 1 - - -
S. sequoyahi	0 0 0 0 1 1 0 0 0 0 1 0 0 0 1 1 0 0 0 1 0 0 0 1 1 1 0 1 1 1 0 0 0 1 1 1 0 1 1 1 0 1 0 1 0 1 1 0 0 0 0 0 0 1 1 1 0
S. tianschanica	0 0 1 1 0 1 0 0 0 1 - - - - - - 0 0 0 1 0 - 0 1 1 1 0 1 0 1 0 0 0 0 1 0 0 1 1 1 1 0 0 0 1 1 1 0 0 0 1 1 1 1 - - -
S. trispinosa	0 0 * 1 0 1 0 0 0 1 1 0 1 0 0 0 0 1 0 1 0 0 0 1 1 0 1 1 1 1 1 0 0 0 1 0 0 1 1 1 1 1 0 0 1 1 1 0 0 0 0 0 0 0 1 0 0
S. unispinosa	0 0 1 1 0 1 0 0 0 1 1 0 1 0 0 0 0 1 0 1 0 0 0 1 1 0 1 1 1 1 1 0 0 0 1 0 0 1 1 1 1 1 0 0 1 1 1 0 0 0 0 1 0 1 1 0 0

Systematics

Class Copepoda H. Milne Edwards, 1840

Order Harpacticoida G.O. Sars, 1903

Family Ameiridae Monard, 1927

Genus *Kimberleynitocrella* gen. nov.

Diagnosis. Large and slender Ameiridae, with cylindrical habitus and no distinct demarcation between prosome and urosome. Integument weakly chitinized and without cuticular windows; hyaline fringe of all somites smooth. First pedigerous somite incorporated into cephalothorax. Prosome weakly ornamented with moderately large sensilla, urosome additionally ornamented with posteroventral rows of small spinules. Genital double-somite without visible suture but slightly constricted laterally; genital field with single large copulatory pore, wide copulatory duct and two small semicircular seminal receptacles; single small genital aperture covered by fused reduced sixth legs, without armature or ornamentation. Anal operculum wide and convex, not reaching to posterior end of anal somite, ornamented with more than 50 minute spinules near posterior margin. Caudal rami conical, as long as greatest width and slightly divergent; dorsal seta inserted near posterior margin and very close to inner margin, about twice as long as ramus; proximal lateral seta arising somewhat dorsolaterally at midlength; distal lateral seta arising at 5/6 and laterally; inner apical seta as long as ramus; principal apical setae with breaking plane. Antennula long and slender, eight-segmented in female and ten-segmented and not strongly geniculate in male; with smooth seta on first segment. Antenna composed of coxa, basis, two-segmented endopod and one-segmented exopod; exopod armed with three setae. Labrum with narrow and convex cutting edge. Mandibula with narrow cutting edge and two-segmented palp; basis unarmed, endopod with four apical setae. Maxillular endopod absent. Maxilla with single endite on syncoxa; endopod a minute, but distinct segment. Maxilliped three-segmented, armed with one seta on syncoxa and one on endopod. All swimming legs with three-segmented exopod. Endopod of first leg three-segmented; endopod of second and third swimming legs two-segmented, while endopod of fourth swimming leg reduced to a small knob. All exopodal segments of about same length; first exopodal segment of all legs without inner seta, second with inner seta; third exopodal segment of first leg with three outer spines and no inner setae, that of other legs with two outer spines and one (second and third leg) or two (fourth leg) inner setae. First endopodal segment of first leg large, about 2.8 times as long as wide, almost reaching to middle of third exopodal segment and armed with short spiniform inner seta; first endopodal segment of other legs small and unarmed. Basis of first leg in male with inner spine transformed, smooth and inflated distally; no other sexual dimorphism in the swimming legs. Fifth leg same in both sexes, represented only by two lateral knobs on surface of somite; inner knob, representing exopod, armed with four smooth and slender setae; outer knob represents outer part of basis and armed with single seta; endopodal lobe absent. Sixth legs in male fused basally together and to somite, each armed with single seta posterolaterally.

Type and only species. *Kimberleynitocrella billhumphreysi* **sp. nov.**

Etymology. The genus name comes from the Kimberley region in Western Australia, where the type species was found, prefixed to the existing genus name *Nitocrella*. Gender feminine.

Kimberleynitocrella billhumphreysi sp. nov.
(Figs 1–4)

Type material. Holotype, adult female dissected on two slides (WAM C37326); paratypes: one adult female dissected on one slide (WAM C37327) and two copepodids preserved in 70% ethanol (WAM C37328);

Australia, Western Australia, Kimberley region, Argyle Diamond Mine, bore MB13, 10 October 2002, leg. W.F. Humphreys and R. Webb (sample BES: 9698), 16°43’18”S 128°24’02”E.

Other material examined. One adult female in 70% ethanol (WAM C37329); Australia, Western Australia, Kimberley region, Argyle Diamond Mine, bore MB13S, 10 October 2002, leg. W.F. Humphreys and R. Webb (sample BES: 9752), 16°43’18”S 128°24’03”E.

One adult male dissected on one slide (WAM C37330); one adult male and one adult female preserved in 70% ethanol (WAM C37331); Australia, Western Australia, Kimberley region, Argyle Diamond Mine, bore B13S, 10 October 2002, leg. W.F. Humphreys and R. Webb (sample BES: 10015), 16°43’18”S 128°24’01”E.

One adult female dissected on two slides (WAM C37332); one adult female preserved in 70% ethanol (WAM C37333); Australia, Western Australia, Kimberley region, Argyle Diamond Mine, bore MB29S, 14 October 2002, leg. W.F. Humphreys and R. Webb (sample BES: 9759), 16°41’37”S 128°27’11”E.

One adult male dissected on one slide (WAM C37334); one adult male preserved in alcohol (WAM C37335); Australia, Western Australia, Ord River, bore WP10, pump 100–200, depth 27.35 m, 26 November 2004, leg. P. Hancock (sample ORIN37); 15°27’52”S 128°53’34”E.

Description. FEMALE (HOLOTYPE). Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding appendages and caudal setae), 0.895 mm. Preserved specimen colourless. Nauplius eye absent. Habitus (Figs 1A–B) cylindrical, slender, without distinct demarcation between prosome and urosome; prosome/urosome ratio 0.7; greatest width at posterior end of cephalothorax. Body length/width ratio about 5.3; cephalothorax 1.2 times as wide as genital double-somite. Free pedigerous somites without pronounced lateral or dorsal expansions. Integument weakly chitinized and without cuticular windows. Rostrum very small, membranous, ovoid, about as long as wide and not demarcated at base; ornamented with two dorsal sensilla.

Cephalothorax (Fig. 1A) incorporating first prosomite, trapezoidal in dorsal view, about as long as wide; represents about 19% of total body length. Surface of cephalic shield and tergites of first three free pedigerous somites ornamented with few small sensilla. Hyaline fringe of all prosomites narrow and smooth. Fifth pedigerous (first urosomal) somite ornamented posteriorly with two dorsal sensilla and two lateral sensilla (one on each side); hyaline fringe smooth both dorsally and laterally, weakly discernible ventrally. Sclerotized joint present ventrally, but not dorsally, between fifth pedigerous and genital double somites.

Genital double-somite (Figs 1A–B, 2A) as long as wide (ventral view), without visible suture but slightly constricted laterally at 2/5; ornamented with eight large dorsal sensilla (four at middle, four near posterior margin), four posterior ventral sensilla and one long and two short transverse rows of small spinules between medial ventral sensilla. Hyaline fringe completely smooth. Genital field with single large copulatory pore (at about 3/7 of double-somite’s length), weakly sclerotized wide copulatory duct and two small semicircular seminal receptacles. Single small genital aperture covered by fused reduced sixth legs, represents 36% of somite width. Third urosomite ornamented with six large sensilla near posterior margin (two dorsal and four ventral) and single posterior ventral row of minute spinules; hyaline fringe smooth. Preanal somite with smooth hyaline fringe; ornamented only with very short posterior ventral row of small spinules. Anal somite (Figs 1A–B, 2A) ornamented with pair of large dorsal sensilla and transverse row of small spinules along posterior margin, those on each corner near anal operculum somewhat longer. Anal operculum (Fig. 3A) convex, not reaching to posterior end of anal somite, represents 52% of somite's width; ornamented near its posterior margin with 56 minute spinules of significantly smaller size than spinules on posterior dorsal margin of anal somite. Anal sinus smooth and widely opened.

Caudal rami (Figs 2A–2B, 3B–3C) short, as long as greatest width (ventral view), conical, slightly divergent, with space between them more than one ramus width; armed with seven armature elements (three lateral, one dorsal and three apical). Ornamentation consists of two minute spinules at base of dorsal seta, two larger spinules at base of distal lateral seta and posterior row of six to eight spinules ventrally. Dorsal seta smooth, inserted near posterior margin and very close to inner margin, about twice as long as caudal ramus, triarticulate at base (i.e. inserted on two pseudojoints). Proximal lateral seta about 0.6 times as long as dorsal one, arising somewhat dorsolaterally at middle of ramus length. Distal lateral seta smooth, arising at 5/6 of

ramus length, about as long as dorsal one. Inner apical seta small, smooth, about as long as ramus. Middle apical seta strongest, with breaking plane, ornamented with minute spinules along both margins from about first quarter to midlength, twice as long as outer apical seta and more than half as long as body. Outer apical seta with breaking plane, ornamented with several minute spinules only on outer margin.

Antennula (Fig. 2C) eight-segmented, unornamented, slender, approximately 1.4 times as long as cephalothorax. Strong aesthetasc on fourth segment fused basally with adjacent large seta and reaches beyond tip of appendage for less than half length of last segment; slender apical aesthetasc on eighth segment fused basally with two apical setae. Setal formula: 1.9.6.4.2.3.4.7. All setae smooth, without breaking plane and uniarticulate at base. Length ratio of antennular segments, from proximal to distal end and along caudal margin, 1 : 1.5 : 1.1 : 1.3 : 0.6 : 0.8 : 0.5 : 1.1.

Antenna (Fig. 1D) composed of coxa, basis, two-segmented endopod and one-segmented exopod. Coxa very short, unarmed and unornamented. Basis about 1.7 times as long as wide, unarmed but ornamented with row of small spinules along anterior margin. First endopodal segment about 2.2 times as long as wide and 1.2 times as long as basis, unornamented and unarmed. Second endopodal segment longest, 1.6 times as long as first and 4.3 times as long as wide, armed medially at 3/4 with two unipinnate spines flanking thin seta; apical armature consisting of five geniculate setae, longest one fused basally to additional smaller seta bearing proximal tuft of fine setules; ornamentation consists of few spinules along anterior surface. Exopod one-segmented, half as long as basis and 2.2 times as long as wide, unornamented but armed with three pinnate setae; innermost apical seta bipinnate, nearly three times as long as other two subequal setae and twice as long as exopod; other two setae with apical tuft of closely packed setules.

Labrum (Fig. 1E) not very large compared with cephalothorax, trapezoidal, rigidly sclerotized, with relatively narrow and slightly convex cutting edge, ornamented with one apical row of small spinules in between two subapical rows of strong spinules (eight on each side). Two small round fields of gustatory papillae visible on dorsal (posterior) surface.

Paragnaths not observed in satisfactory position.

Mandibula (Fig. 1F) with narrow cutting edge on elongated coxa, armed with coarser teeth at ventral half, finer teeth at dorsal half and one dorsal unipinnate seta. One short row of spinules present on outer part of coxa. Palp uniramous, comprising basis and one-segmented endopod. Basis unarmed and unornamented, 1.5 times as long as wide. Endopod slender and unornamented, about 1.3 times as long as basis and 3.2 times as long as wide; armed with five slender smooth apical setae.

Maxillula (Fig. 1G) with large praecoxa; arthrite rectangular, not movable, ornamented with arched row of spinules ventrally and armed with two smooth setae on anterior surface, two setae on dorsal margin and four apical elements (probably three spines and one dorsal seta; dorsal seta ornamented with two long setules). Coxal endite armed apically with one pinnate, strong and recurved seta dorsally and two smooth slender setae ventrally, all of about same length. Basis somewhat shorter than coxal endite, armed with four apical smooth setae and one subapical smooth seta. Endopod absent.

Maxilla (Fig. 1H) with proximal syncoxal endite absent; distal endite well developed, highly mobile, armed with one curved and basally fused, bipinnate spine and two smooth subequal setae, which 1.4 times as long as spine. Basis drawn out into long and nearly straight claw, with shorter spiniform curved seta at its base; no cuticular pore or other ornamentation observed. Endopod represented by minute segment, armed with two smooth subequal, long apical setae.

Maxilliped (Fig. 1I) with well developed syncoxa, 1.8 times as long as wide, unornamented and armed with single smooth seta subapically. Basis 2.5 times as long as wide and almost 1.2 times as long as syncoxa, unarmed but ornamented distolaterally with short transverse row of small spinules. Endopod represented by long and slightly curved claw, ornamented distally with row of spinules along concave side; with thin seta at base.

All swimming legs with three-segmented exopod; endopod of first leg three-segmented (Fig. 3D), endopod of second and third swimming legs two-segmented (Figs 2D, 3E), while endopod of fourth swimming leg reduced to small knob (Fig. 3F). Armature formula of swimming legs as follows (for

preultimate segments—inner/outer elements; for ultimate segments—inner/terminal/outer elements):

	Exopod			Endopod		
Segments	1	2	3	1	2	3
First leg	0/1	1/1	0/2/3	1/0	0/0	1/1/1
Second leg	0/1	1/1	1/2/2	0/0	(2)/1/1	-
Third leg	0/1	1/1	1/2/2	0/0	1/1/1	-
Fourth leg	0/1	1/1	2/2/2	-	-	-

Intercoxal sclerite of all swimming legs with concave distal margin and without surface ornamentation. Praecoxae of all legs very short and unornamented. Coxa of first swimming leg ornamented with several long spinules on inner distal margin, that of other legs unornamented; all coxae unarmed. Basis of first leg ornamented posteriorly with arched row of spinules along anterior surface of endopod base; second leg with row of spinules near outer margin; third and fourth legs with spinules only along outer margin; each leg armed with slender smooth seta on outer margin (longest one on third leg); first leg with short stout spine on inner distal corner. All exopodal and endopodal segments ornamented with strong spinules along outer margin; some segments also with spinules along inner and distal margins. All exopodal segments of about same length. First endopodal segment of first swimming leg (Fig. 3D) large, about 2.8 times as long as wide and almost reaching to midlength of third exopodal segment; endopod longer than exopod, reaching beyond distal margin of exopod for length of last endopodal segment. Endopod of second swimming leg (Fig. 2D) reaching to midlength of second exopodal segment; its second segment twice as long as first. Endopod of third leg (Fig. 3E) as long as first exopodal segment; its second segment twice as long as first. Endopod of fourth swimming leg (Fig. 3F) reduced to tiny knob, without armature or ornamentation. All setae on each ramus (except minute inner seta on third endopodal segment of first leg) strong and many also spiniform.

Fifth leg (Figs 1B & J–K) represented only by two unornamented but armed lateral knobs on surface of somite. Inner knob, representing exopod, armed with four smooth slender setae; outermost seta strongest and longer than other three. Outer knob represents outer part of basis and armed with long unipinnate seta; this seta much longer than any seta on inner knob. Endopodal lobe absent.

Sixth legs (Fig. 2A) completely fused together, indistinct, forming simple operculum covering single gonopore, without ornamentation or armature.

MALE (WAM C37330). Body length, excluding caudal setae, 0.738 mm. Habitus, ornamentation of prosomites, rostrum, colour and nauplius eye similar to female. Hyaline fringe of all prosomites smooth; no cuticular windows observed.

Genital somite more than twice as wide as long, with single small, longitudinally placed spermatophore visible inside (Fig. 4A). Urosomite ornamentation similar to female, although preanal somite without spinules and second, third and fourth urosomites with additional lateral sensilla.

Anal somite and caudal rami (Fig. 4A) proportions, armature and ornamentation very similar to female, just dorsal sensilla significantly longer.

Antennula (Fig. 4B) long and slender, ten-segmented, not strongly geniculate, with geniculation between seventh and eighth segments; ornamented with arched row of spinules only on first segment anteroproximally. Aesthetasc on apical acrothek of fifth segment very long and broad (homologous to aesthetasc on fourth segment in female); smaller aesthetasc on tenth segment fused basally to two apical setae. First two and last two segments similar to female. Setal formula: 1.9.7.1.8.1.2.1.4.7. Most setae smooth and slender; two setae on fifth segment and one on sixth very short, strong and unipinnate; proximal seta on seventh segment unipinnate, strong and relatively long. Just two setae on ninth segment and three lateral setae on tenth segment biarticulating on basal part; all other setae uniarticulate; all setae without breaking plane.

Antenna, labrum, mandibula, maxillula, maxilla, maxilliped and second (Fig. 4D) and fourth swimming legs (Fig. 4F) similar to female.

First swimming leg (Fig. 4C) with inner spine on basis significantly modified, smooth and inflated distally.

FIGURE 1. *Kimberleynitocrella billhumphreysi* **gen. et sp. nov.**, holotype female: A—habitus, dorsal view; B—habitus, lateral view; C—principal apical caudal setae; D—antenna; E—labrum; F—mandibula; G—maxillula; H—maxilla; I—maxilliped; J—right fifth leg; K—left fifth leg. Scales = 0.1 mm.

FIGURE 2. *Kimberleynitocrella billhumphreysi* **gen. et sp. nov.**, holotype female: A—urosome, ventral view; B—left caudal ramus, lateral view; C—antennula; D—left second swimming leg and endopod of right leg. Scales = 0.1 mm.

FIGURE 3. *Kimberleynitocrella billhumphreysi* **gen. et sp. nov.**, A–F, holotype female; G & H, paratype female (0.846 mm): A—anal operculum; B—left caudal ramus, dorsal view; C—right caudal ramus, ventral view; D—first swimming leg; E—third swimming leg; F—fourth swimming leg; G—endopod of second swimming leg; H—endopod of third swimming leg. Scale = 0.1 mm.

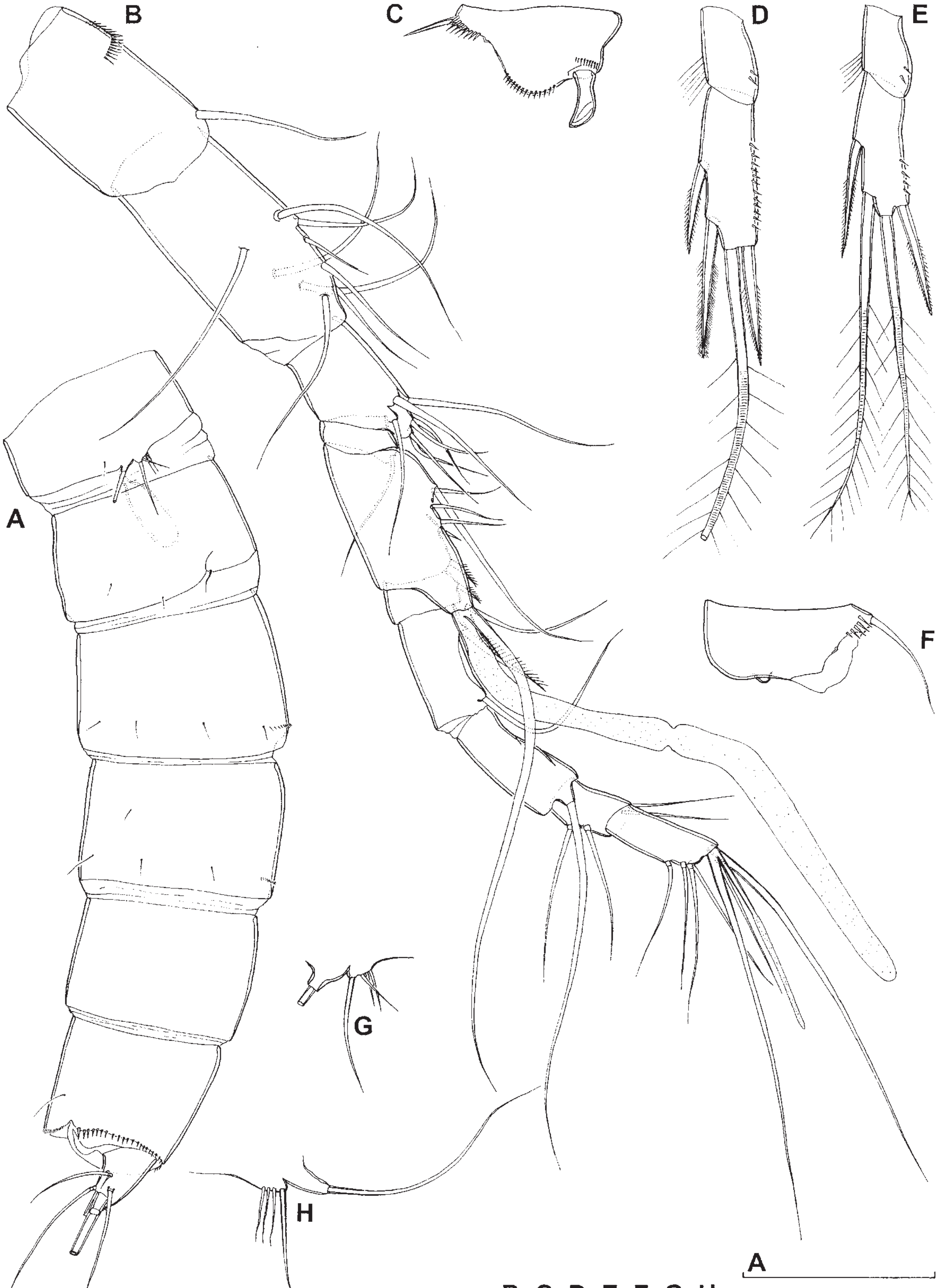

FIGURE 4. *Kimberleynitocrella billhumphreysi* **gen. et sp. nov.**, male (WAM C37330; 0.738 mm): A—urosome, lateral view; B—antennula; C—basis of first swimming leg; D—endopod of second swimming leg; E—endopod of third swimming leg; F—basis of fourth swimming leg; G—right fifth leg; H—left fifth leg. Scales = 0.1 mm.

Third swimming leg (Fig. 4E) with inner distal seta on second endopodal segment plumose and slender, not spiniform and bipinnate as in female; other details similar to female.

Fifth leg (Figs 4G–H) remarkably similar to female, except outer basal seta smooth and outer exopodal seta somewhat stronger.

Sixth legs (Fig. 4A) fused together medially, indistinct from somite and each armed with single small smooth seta, about as long as smaller exopodal setae on fifth leg.

Variability. Body length of females ranges from 0.815 mm to 0.895 mm (0.849 mm average; n = 6), while in males it ranges from 0.738 mm to 0.754 mm (0.742 mm average; n = 4). The holotype female has an asymmetrical endopod of the second swimming leg (Fig. 2D), with one or two inner spiniform setae on the second segment. All other specimens have two inner spiniform setae on the second endopodal segment of the second swimming leg (Figs 3G, 4D). Second endopodal segment of the third swimming leg in both males and females can be with (Figs 3H, 4E) or without (Fig. 3E) an inner spiniform seta. Small differences in ornamentation of the swimming legs were also observed, as well as in the proportions of the last endopodal segment especially when they carry different armature elements (Figs 3E & H). The fifth legs (Figs 1J–K) are also slightly asymmetrical in the holotype, particularly the length of the outermost exopodal seta. Other female and male (Figs 4G–H) specimens have their fifth legs less asymmetrical. The number of minute spinules on the anal operculum can also vary, but they are always smaller than those along the posterior margin of the anal somite next to the operculum.

Etymology. The species is named in honour of Dr William F. Humphreys (Western Australian Museum), who collected the type material. The name is a noun in the genitive singular.

Remarks. Reduction of the endopod of the fourth swimming leg to a minute knob is known only in three other ameirid harpacticoids: two species of the genus *Psammonitocrella* Huys, 2009, described from Arizona (USA) by Rouch (1992), and the type and only species of the genus *Neonitocrella* Lee & Huys, 2002, described by Miura (1962) from Japan. However, it is more than likely that this reduction may have occurred independently, as a result of convergence or parallelism (homoplasy), between these two genera and *Kimberleynitocrella* **gen. nov.** considering that they do not share any other synapomorphies.

The genus *Kimberleynitocrella* **gen. nov.** also has very reduced fifth legs (although all four exopodal setae are still present; their slender nature and close position to the outer basal seta reveal their exopodal rather than endopodal origin), as well as some unusual reductions in the mouth appendages (the absence of the endopod of the maxillula, for example), but it stands apart from the other ameirids studied here mostly because of its plesiomorphic characters: three outer spines on the third exopodal segment of the first leg; inner seta present on the second exopodal segment of the first leg; third exopodal segment of the second and third legs with one inner seta and that of the fourth leg with two inner setae; endopod of the second and third leg two-segmented; and most importantly, endopod of the second and third legs with three or four armature elements, which include the outermost subapical spine, ancestral outer apical seta and one or two inner (lateral) elements. These, and some other plesiomorphic characters in the antennula, antenna and genital double-somite in female, clearly define *Kimberleynitocrella* **gen. nov.** as a sister group of the remaining *Stygonitocrella s. l.* species and, in combination with previously mentioned apomorphic features, support its separate generic status.

Clearly, this strange ameirid had to evolve from an ancestor that was even more primitive than most recent freshwater representatives of this family, possibly from a marine or brackish *Nitocra* Boek, 1865 species. This and some other plesiomorphic features observed in other *Stygonitocrella s. l.* species presented here, prompted us to choose *Biameiropsis barrowensis* Karanovic, 2006 as the outgroup for the cladistic analysis presented in this paper, because this anchialine ameirid has most characters in their plesiomorphic state and will also be a suitable outgroup for any future cladistic analyses of other freshwater ameirid genera.

Genus *Gordanitocrella* gen. nov.

Diagnosis. Medium sized, slender Ameiridae, with cylindrical habitus and no distinct demarcation between prosome and urosome. Integument weakly chitinized and without cuticular windows; hyaline fringe of all prosomites smooth, those of urosomites finely serrated. First pedigerous somite incorporated into cephalothorax. Prosome ornamented with very large sensilla, urosome additionally ornamented with rows of small spinules. Genital double-somite without visible suture or lateral constriction; genital field with single small copulatory pore, narrow and short copulatory duct and two large semicircular seminal receptacles; single small genital aperture covered by fused reduced sixth legs. Anal operculum wide and convex, not reaching to posterior end of anal somite, ornamented with nearly 30 spinules near posterior margin. Caudal rami slender, about twice as long as greatest width, nearly cylindical, with space between them more than 1.5 times as wide as one ramus, with small diagonal chitinous ridge dorsally and ventral posterior margin produced somewhat inwards; dorsal seta inserted close to inner margin, 1.7 times as long as caudal ramus; proximal and distal lateral setae smooth and of about same length, 0.6 times as long as dorsal seta; principal apical setae with breaking plane. Antennula long and slender, eight-segmented in female and ten-segmented and strongly geniculate in male, with unipinnate seta on first segment. Antenna composed of coxa, basis, two-segmented endopod and one-segmented exopod; exopod armed with two setae. Labrum with convex cutting edge. Mandibula with narrow cutting edge and two-segmented palp; basis unarmed, endopod with four apical setae. Maxillular endopod armed with one apical seta. Maxilla with single endite on syncoxa; endopod minute, armed with two setae. Maxilliped three-segmented, armed with one seta on syncoxa and one on endopod. All swimming legs with three-segmented exopod. Endopod of first leg three-segmented; endopod of other legs one-segmented. All exopodal segments of about same length; first exopodal segment of all legs without inner seta, second with inner seta; third exopodal segment of first leg with three outer spines and no inner setae, that of other legs with two outer spines and one inner seta. First endopodal segment of first leg large, reaching to 3/4 of second exopodal segment, armed with short spiniform inner seta; endopod of second leg with two setae, third leg with three and fourth leg with one apical plumose seta. Inner distal corner of basis produced into short chitinous process at base of inner spine in both sexes; inner spine transformed, smooth and inflated distally, in male; no other sexual dimorphism in swimming legs. Fifth leg biramous but baseoendopod fused medially together and to somite; endopodal lobe not recognizable, forming straight smooth hyaline fringe and without armature or ornamentation; exopod distinctly one-segmented in female but fused basally together and to somite in male, small, armed with three slender smooth setae in female and with additional inner spine on male right leg. Sixth legs in male fused basally together and to somite, each armed with two smooth setae posterolaterally.

Type and only species. *Gordanitocrella trajani* **sp. nov.**

Etymology. The genus name is dedicated to Prof Gordan S. Karaman (University of Montenegro), one of the mentors of the senior author, as a celebration of his 70th birthday and 50 years of his scientific work. His first name is prefixed to the existing genus name *Nitocrella*. Gender feminine.

Gordanitocrella trajani sp. nov.
(Figs 5–7)

Type material. Holotype, adult female dissected on one slide (WAM C37336); allotype, adult male dissected on one slide (WAM C37337); paratypes: one adult female and one male dissected together on one slide (WAM C37338), one adult female and one male together on one slide *in toto* (WAM C37339), five males, three females and one copepodid preserved in 70% ethanol (WAM C37340); Australia, Western Australia, Pilbara region, N of Newman, bore Corktree, depth 31 m, 29 October 2006, leg. P. Hancock (Jar no. FMG36), 22°47’32”S 119°18’34”E.

Other material examined. One adult male dissected on one slide (WAM C37341); one adult female and three copepodids preserved in 70% alcohol (WAM C37342); Australia, Western Australia, Pilbara region, near Weeli Wolli spring, bore HD11D, 17 November 2003, leg. J. Cocking & M. Scanlon, 20°57'06"S 119°09'23"E.

One adult female dissected on one slide (WAM C37343); one adult female and one copepodid preserved in 70% alcohol (WAM C37344); Australia, Western Australia, Pilbara region, Pebble Mouse Creek, bore WB3, 17 November 2003, leg. J. Cocking & M. Scanlon, 23°00'09"S 119°07'56"E.

Description. FEMALE (HOLOTYPE). Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding appendages and caudal setae), 0.563 mm. Preserved specimen colourless. Nauplius eye absent. Habitus (Figs 5A–B) cylindrical, slender, without distinct demarcation between prosome and urosome; prosome/urosome ratio 0.85; greatest width at first free pedigerous somite. Body length/width ratio about 5.3; cephalothorax only 1.1 times as wide as genital double-somite. Free pedigerous somites without pronounced lateral or dorsal expansions. Integument not strongly chitinized and without cuticular windows. Rostrum (Fig. 5A) small and membranous, linguiform, reaching to just beyond proximal third of first antennular segment, about twice as long as wide and not demarcated at base; ornamented with two dorsal sensilla near anterior margin.

Cephalothorax (Fig. 5A) with completely incorporated first pedigerous somite, almost cylindrical in dorsal view, somewhat longer than wide; represents 21% of total body length. Surface of cephalic shield and tergites of three free pedigerous somites ornamented only with large sensilla. Hyaline fringe of all prosomites narrow and smooth. Fifth pedigerous (first urosomal) somite ornamented posteriorly with two large dorsal sensilla and two smaller lateral sensilla (one on each side); hyaline fringe finely serrated dorsally and laterally, smooth ventrally (Figs 5B–C). Large sclerotized joint (Figs 5A–C) present between fifth pedigerous and genital double somites and visible both ventrally and dorsally.

Genital double-somite (Fig. 5C) 0.8 times as long as wide (ventral view), without visible suture and only slightly wider at anterior part; ornamented with two large sensilla dorsally, two sensilla ventrally, two small cuticular pores laterally (one on each side), one short transverse row of minute spinules at dorsal midline and uninterrupted posterior row of spinules, those on ventral side larger. Hyaline fringe finely serrated both ventrally and dorsally. Genital field with single small copulatory pore, narrow sclerotized copulatory duct and two semicircular seminal receptacles, posterior part of which reaches beyond copulatory pore. Copulatory pore situated slightly posterior from proximal fourth of double-somite length. Single small genital aperture covered by fused reduced sixth legs, represents 40% of somite width. Third urosomite ornamented also with four large sensilla near posterior margin (two dorsal and two ventral), uninterrupted posterior row of spinules and two lateral pores, but additionally ornamented ventrally with four cuticular pores (two at anterior and two at posterior part) and short and slightly interrupted transverse row of minute spinules between posterior pores, very close and parallel to posterior row; hyaline fringe finely serrated. Preanal somite with finely serrated hyaline fringe dorsally and ventrally, ornamented with continuous posterior row of spinules and one additional row of spinules and two pores ventrally. Anal somite (Figs 5B–C, 6A) ornamented with pair of large dorsal sensilla, two lateral and four ventral cuticular pores, short transverse row of minute spinules at lateral 2/3, interrupted and arched row of minute spinules ventrally at 1/3 and posterior row of somewhat larger spinules, interrupted ventrally between caudal rami. Anal operculum convex, not reaching to posterior end of anal somite, represents 57% of somite's width; ornamented near its posterior margin with 29 spinules of about same size as spinules on posterior dorsal margin. Anal sinus widely opened, ornamented with two diagonal rows of minute spinules.

Caudal rami (Figs 5B–C, 6A, 7A) slender, about twice as long as greatest width (ventral view), nearly cylindical, clearly convergent, with space between them more than 1.5 times as wide as one ramus, with small diagonal chitinous ridge dorsally and ventral posterior margin produced somewhat inwards; armed with seven armature elements (three lateral, one dorsal and three apical). Ornamentation consists of several small spinules at base of dorsal and distal lateral seta, one ventral and two lateral pores and posterior ventral row of five larger spinules. Dorsal seta smooth, inserted close to inner margin, at about 2/3 of ramus length, 1.7 times

as long as caudal ramus, biarticulate at its base. Proximal and distal lateral setae smooth and of about same length, 0.6 times as long as dorsal one; proximal seta arising somewhat dorsolaterally and slightly more anteriorly than dorsal seta; distal lateral seta arising at 4/5 of ramus length. Inner apical seta very slender and small, smooth, about 0.6 times as long as ramus. Both principal setae broken at breaking plane and inserted more dorsally than apically.

Antennula (Fig. 6B) eight-segmented, slender, approximately 1.3 times as long as cephalothorax. Long and relatively slender aesthetasc on fourth segment reaches beyond tip of appendage for length of last three segments combined and fused basally with large subapical seta; much smaller and even more slender apical aesthetasc on eighth segment fused basally to two apical setae. Setal formula: 1.8.6.3.2.2.4.7. Only seta on first segment unipinnate, all other setae smooth. Only four setae on eighth segment articulating on basal part; all setae without breaking plane. First segment ornamented with short row of long spinules at middle of anterior surface; other segments without ornamentation. Length ratio of antennular segments, from proximal to distal end and along caudal margin, 1 : 1.7 : 1 : 1 : 0.5 : 0.6 : 0.4 : 0.8.

Antenna (Fig. 5D) composed of coxa, basis, two-segmented endopod and one-segmented exopod. Coxa very short, unornamented. Basis about 1.7 times as long as wide, unarmed but ornamented with two short rows of long spinules along anterior margin. First endopodal segment slightly longer and more slender than basis, unornamented and unarmed. Second endopodal segment longest, 1.5 times as long as first and 3.6 times as long as wide, armed medially with two smooth spines flanking thin seta; apical armature consisting of five geniculate setae, longest one fused basally to additional smaller seta bearing proximal tuft of fine setules; ornamentation consists of few spinules along anterior surface and two fringes on posterior surface. Exopod one-segmented, small, 0.4 times as long as basis and 2.7 times as long as wide, unornamented but armed with two setae; inner seta bipinnate, slender, arising apically, 1.7 times as long as outer one and almost 2.5 times as long as exopod; outer seta curved, unipinnate and much stronger than inner seta.

Labrum (Fig. 5E) large compared to cephalothorax, trapezoidal, rigidly sclerotized, with relatively broad and convex cutting edge, ornamented with one apical row of small spinules in between two subapical rows of strong spinules. Two ellipsoid fields of gustatory papillae visible on dorsal (posterior) surface.

Paragnaths (Fig. 5F) ovoid, fused basally into trapezoidal labium; each ornamented with apical row of spinules (which becomes smaller towards inner margin), one spinule on outer margin and longitudinal row of four large curved spinules at middle, close to inner margin.

Mandibula (Figs 5G–H) with narrow cutting edge on elongated coxa, armed with numerous small teeth in between three ventral coarse teeth and one dorsal unipinnate seta. Palp uniramous, comprising basis and one-segmented endopod. Basis slender, unarmed and unornamented, 2.5 times as long as wide and 1.7 times as long as endopod. Endopod also slender and unornamented, about twice as long as wide; armed apically with five slender smooth setae.

Maxillula (Fig. 5I) with large praecoxa; arthrite rectangular, not movable, unornamented, armed with two smooth setae on anterior surface, three setae on dorsal margin and four apical elements (probably three spines and one seta). Coxal endite shorter than praecoxal arthrite, armed apically with one curved pinnate and two slender smooth setae, all of about same length. Basis about as long as coxal endite, armed with four smooth setae apically and one smooth seta subapically. Endopod a minute but distinct segment, armed with minute smooth apical seta.

Maxilla (Fig. 5J) with proximal syncoxal endite absent; distal endite well developed, highly mobile, armed with one pinnate spine and two smooth setae (middle seta nearly twice as long as other two elements). Basis drawn out into long claw, with much shorter spiniform curved seta at its base. Endopod represented by minute segment, armed with two smooth subequal, long apical setae.

Maxilliped (Fig. 5K) with well developed syncoxa, ornamented with several minute spinules at inner distal corner and armed with single smooth seta near outer distal corner, 1.8 times as long as wide. Basis 2.8 times as long as wide and almost 1.3 times as long as syncoxa, unarmed but ornamented with interrupted row of small spinules along inner margin. Endopod represented by long curved claw, ornamented distally with row of spinules along concave side; with thin seta at base.

FIGURE 5. *Gordanitocrella trajani* **gen. et sp. nov.**, holotype female: A—habitus, dorsal view; B—habitus, lateral view; C—urosome, ventral view; D—antenna; E—labrum; F—paragnaths; G—cutting edge of mandibula; H—mandibular palp; I—maxillula; J—maxilla; K—maxilliped. Scales = 0.1 mm.

FIGURE 6. *Gordanitocrella trajani* **gen. et sp. nov.**, A–H, holotype female; I, paratype female (0.571 mm); J–L, paratype female (0.562 mm): A—anal somite and caudal rami, dorsal view; B—antennula; C—first swimming leg; D—second swimming leg; E—right endopod of third swimming leg; F—left endopod of third swimming leg, without armature; G—fourth swimming leg; H—left fifth leg; I—left fifth leg; J—endopod of second swimming leg; K—endopod of third swimming leg; L—left fifth leg. Scale = 0.1 mm.

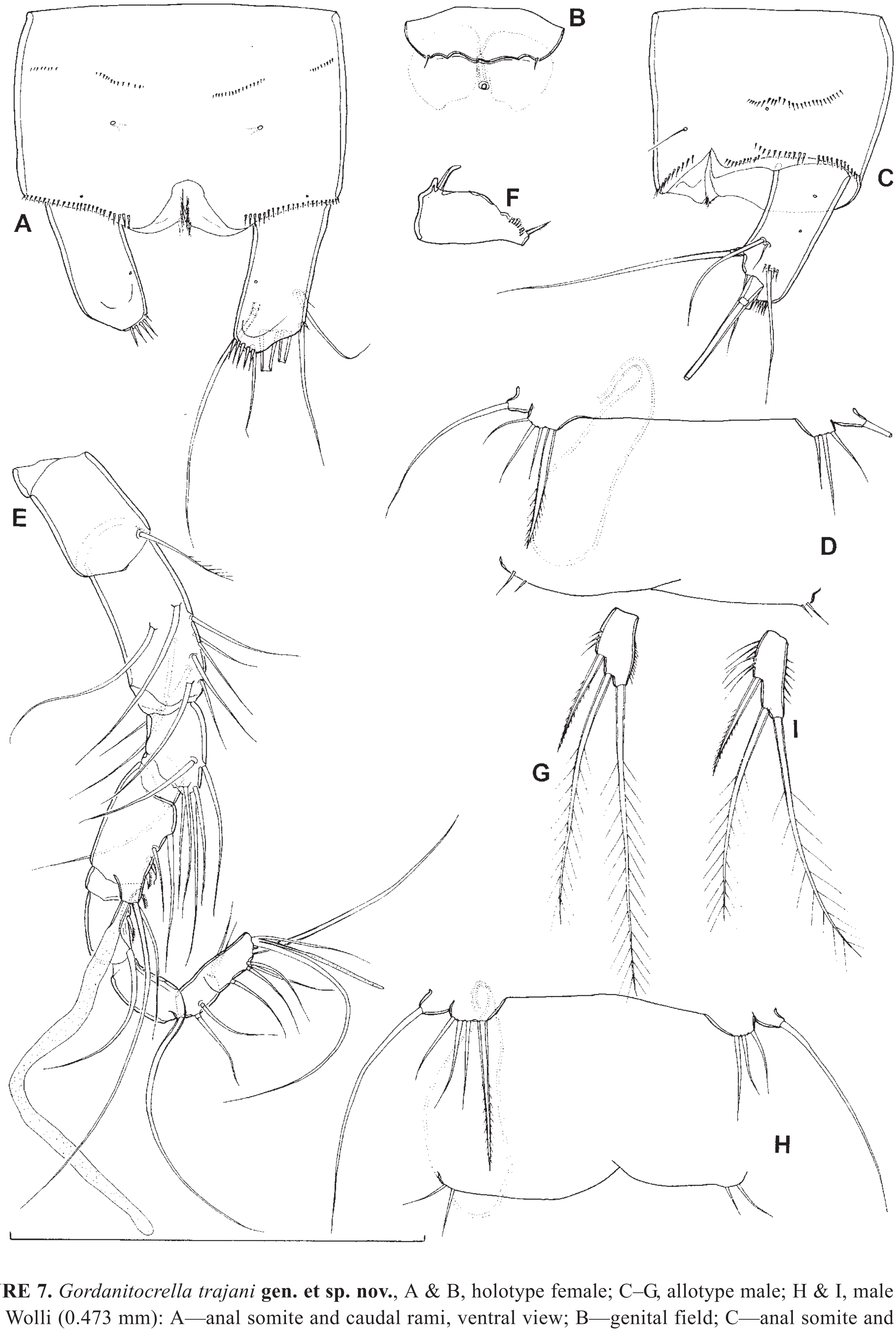

FIGURE 7. *Gordanitocrella trajani* **gen. et sp. nov.**, A & B, holotype female; C–G, allotype male; H & I, male from Weeli Wolli (0.473 mm): A—anal somite and caudal rami, ventral view; B—genital field; C—anal somite and right caudal ramus, lateral view; D—fifth and sixth legs, with spermatophore visible inside; E—antennula; F—basis of first swimming leg; G—endopod of third swimming leg; H—fifth and sixth legs, with spermatophore visible inside; I—endopod of third swimming leg. Scale = 0.1 mm.

All swimming legs with three-segmented exopod; endopod of first leg three-segmented (Fig. 6C), endopod of other swimming legs one-segmented (Figs 6D–G). Armature formula of swimming legs as follows (inner/outer element; inner/terminal/outer element):

	Exopod			Endopod		
Segments	1	2	3	1	2	3
First leg	0/1	1/1	0/2/3	1/0	0/0	1/1/1
Second leg	0/1	1/1	1/2/2	1/1/0	-	-
Third leg	0/1	1/1	1/2/2	2/1/0	-	-
Fourth leg	0/1	1/1	1/2/2	0/1/0	-	-

Intercoxal sclerite of all swimming legs with concave distal margin and without surface ornamentation. Praecoxae short and smooth. Coxa of first leg with diagonal row of spinules at inner distal corner, that of other legs smooth; all coxae unarmed. Basis of each leg ornamented with spinules near outer margin, that of first leg additionally with several slender spinules on inner margin; armed with outer pinnate spine on first and second swimming legs and outer smooth seta on third and fourth legs; first leg with stout spine and produced pseudospine structure on inner distal corner. All exopodal and endopodal segments ornamented with slender spinules along inner margin and strong spinules along outer margin and on outer distal corner; inner distal corner of first and second exopodal segments with frilled membrane. All exopodal segments of about same length. First endopodal segment of first swimming leg (Fig. 6C) large, about 2.4 times as long as wide and reaching to 2/3 of second exopodal segment; endopod significantly longer than exopod. Endopod of second and third swimming legs about as long as first exopodal segment; that of fourth leg half as long. All setae on each ramus (except minute inner seta on third endopodal segment of first leg) strong and some also spiniform. Apical armature element(s) on first leg geniculate.

Fifth leg (Figs 5C, 6H) biramous, but baseoendopod fused medially together and to somite. Endopodal lobe not recognizable, forming straight smooth hyaline fringe and without armature or ornamentation. Basal outer seta slender and smooth, on long setophore, which also is fused basally to somite. Exopod a distinct segment, ovoid, small, slightly longer than its maximum width, unornamented and armed with three slender smooth setae; length ratio of exopodal setae slightly different on left and right leg, although innermost seta longest and outermost seta shortest. Longest exopodal seta 0.44 times as long as outer basal seta.

Sixth legs (Fig. 5C) completely fused together, indistinct, forming simple operculum covering single gonopore, without any ornamentation but each armed with single minute seta.

MALE (ALLOTYPE). Body length 0.484 mm. Habitus, ornamentation of prosomites, rostrum, colour and nauplius eye similar to female. Hyaline fringe of all prosomites smooth, those of urosomites finely serrated.

Genital somite twice as wide as long, with small and slender spermatophore longitudinally placed inside fifth pedigerous and genital somites (Fig. 7D). Anal somite with slightly longer lateral row of spinules (Fig. 7C), but otherwise same as in female. Anal operculum with 32 spinules.

Caudal rami (Fig. 7C) slightly more elongated and almost parallel, but armature and ornamentation very similar to female.

Antennula (Fig. 7E) long and slender, ten-segmented, but with last two segments partly fused, unornamented and strongly geniculate, with geniculation between seventh and eighth segments. Aesthetasc on apical acrothek of fifth segment very long and broad (homologous to aesthetasc on fourth segment in female); smaller aesthetasc on tenth segment fused basally to two apical setae. Armature of first, ninth and tenth segments similar to female. Setal formula: 1.10.6.1.6.1.2.1.4.7. Majority of setae smooth and slender; seta on first segment unipinnate and slender; two setae on fifth, one on sixth and one on seventh segment very short, unipinnate and spiniform. Just two lateral setae on ninth and three on tenth segment biarticulate at their base. Setae without breaking plane.

Antenna, labrum, mandibula, maxillula, maxilla, maxilliped and second, third (Fig. 7G) and fourth swimming legs similar to female.

First swimming leg (Fig. 7F) with inner spine on basis modified as smooth, apically curved outwards and slightly inflated element; cuticular protrusion at base of inner spine similar to female; basis without ornamentation on inner margin.

Third swimming leg (Fig. 7G) with inner seta on endopod somewhat shorter and with fewer and smaller pinnules; other details similar to female.

Fifth legs (Fig. 7D) more fused to somite than in female, with smaller exopod completely fused basally to somite; otherwise similar to female. Left exopod armed with three slender setae like in female, while right exopod additionally armed with long and strong spine as innermost element; this spine 1.8 times as long as longest seta on segment.

Sixth legs (Fig. 7D) fused medially together, indistinct from somite, each armed with two smooth short setae; outer seta about 1.7 times as long as inner one.

Variability. Body length of females ranges from 0.560 mm to 0.571 mm (0.565 mm average; n = 9), while in males it ranges from 0.473 mm to 0.493 mm (0.484 mm average; n = 7). The insertion of endopodal elements on the third swimming leg is slightly asymmetrical in the holotype female (Figs 6E–F). One paratype female has the exopod of the left fifth leg with the innermost seta shorter than the middle one and also the outermost seta is inserted further away from the other two than in the holotype female (Fig. 6I). Another paratype female has a somewhat smaller and more rounded exopod of the fifth leg (Fig. 6L), as well as a somewhat more ornamented endopod of the second and third legs (Figs 6J–K). The male from Weeli Wolli has the innermost seta on the third leg endopod inserted more basally than in the allotype (Fig. 7I), but also somewhat longer setae on the sixth legs and a slightly larger spermatophore (Fig. 7H); the fifth legs are also somewhat different from the allotype, especially in the relative length of the setae. Remarkably, all examined males had the additional spine always on the right fifth leg.

Etymology. The species name is dedicated to Dr Trajan K. Petkovski (Natural History Museum of Macedonia), who first recognized and established the genus *Stygonitocrella* in 1976, although he did not designate a type species and thus the name became unavailable under the current Zological Code. The name is a noun in the genitive singular.

Remarks. If we consider only the segmentation of the swimming legs (as was done in the past) this species would fit perfectly into the diagnosis of the genus *Stygonitocrella* Reid, Hunt & Stanley, 2003, with its one-segmented endopod of the second, third and fourth legs. However, a closer examination reveals that *Gordanitocrella trajani* **gen. et sp. nov.** has no close relatives among recent representatives of this group of freshwater ameirids.

For example, while three armature elements on the ultimate endopodal segment of the third leg can be found in three other species of *Stygonitocrella s. l.*, they are not homologous with each other: in *Kimberleynitocrella billhumphreysi* **gen. et sp. nov.** they represent the ancestral outer subapical spine, outer apical seta and distal inner seta (note: middle inner seta also sometimes present in this species), i.e. characters 35, 36 & 38 in Table 2; in *Gordanitocrella trajani* **gen. et sp. nov.** the outer apical seta and middle and distal inner setae are present, i.e. characters 36, 38 & 39; in *Lucionitocrella yalleenensis* **gen. et sp. nov.** the two apical setae and middle inner seta are expressed, i.e. characters 36, 37 & 39; while in *Eduardonitocrella mexicana* (Suárez-Morales & Iliffe, 2005) comb. nov. we find two apical setae and a distal inner seta, i.e. characters 36, 37 & 38. A similar comparison can be made for many other leg segments (see Tables 1 & 2), which shows that these four freshwater ameirids all had an independent evolutionary path, instead of a common origin, from some more primitive forms of this family.

Plesiomorphic features of *G.trajani* place it relatively basal on the phylogenetic tree and relatively close to *K .billhumpheysi* (Fig. 18); they include: an inner seta on the second exopodal segment and three outer spines on the third exopodal segment of the first leg; an inner seta on the third exopodal segment of the second, third and fourth legs; and more than two setae on the ultimate endopodal segment of the third leg. However, unlike *K. billhumphreysi, G. trajani* has a relatively well developed endopod of the fourth leg, which is armed with the ancestral outer apical seta (Table 2, character 44), as well as a distinct exopod of the female fifth leg and the presence of a maxillular endopod. These two species also differ in many other apomorphic characters.

A one-segmented endopod of the second leg armed with an ancestral outer apical seta and distal inner seta (Table 2, characters 26 & 28), would position *G. trajani* close to *L. yalleenensis*, but the latter ameirid has no plesiomorphic features on the third exopodal segment of the first leg, nor inner setae on the third exopodal segment of the second and third legs. Further, *L. yalleenensis* has, unlike any other *Stygonitocrella s. l.*, a plesiomorphic armature on the outer side of the third exopodal segment of the second leg (with three outer spines) and differs from *G. trajani* also in having two armature elements on the endopod of the fourth leg, as well as by many other less important characters in the antenna, fifth leg, caudal rami, etc. The new genus differs from *E. mexicana* even more than from the two Australian genera mentioned here (see below). The only obvious autapomorphic feature of the genus *Gordanitocrella* **gen. nov.** is its inner distal spiniform process on the basis of the first leg in both sexes (Figs 6C, 7F). Caudal rami of this genus are also different from those observed in other members of *Stygonitocrella s. l.,* but it is very hard to formulate these differences into commentable characters.

Genus *Lucionitocrella* gen. nov.

Diagnosis. Small Ameiridae, with cylindrical habitus and no distinct demarcation between prosome and urosome. Integument weakly chitinized and without cuticular windows; hyaline fringe of all somites smooth. First pedigerous somite incorporated into cephalothorax. Prosome weakly ornamented with moderately large sensilla, urosome additionally ornamented with posterior ventral row of small spinules. Genital double-somite without visible suture or lateral constrictions; genital field with single small copulatory pore, narrow copulatory duct and two small triangular seminal receptacles; single small genital aperture covered by fused reduced sixth legs. Anal operculum wide and convex, not reaching to posterior end of anal somite, ornamented with more than 25 minute spinules near posterior margin. Caudal rami slightly longer than their greatest width (ventral view), conical, slightly divergent, with space between them about one ramus width; armed with seven armature elements (three lateral, one dorsal and three apical): dorsal seta inserted near posterior margin and close to inner margin, about twice as long as caudal ramus; lateral setae of about same length, somewhat shorter than dorsal one and also inserted quite close to posterior margin; principal apical setae with breaking plane. Antennula long and slender, eight-segmented in female and ten-segmented and geniculate in male, with smooth seta on first segment. Antenna composed of coxa, basis, two-segmented endopod and one-segmented exopod; exopod minute, armed with one apical seta. Labrum with narrow and convex cutting edge. Mandibula with narrow cutting edge and two-segmented palp; basis unarmed, endopod with four apical setae. Maxillular endopod armed with single apical seta. Maxilla with single endite on syncoxa; endopod minute, armed with two setae. Maxilliped three-segmented, armed with one seta on syncoxa and one on endopod. All swimming legs with three-segmented exopod. Endopod of first leg three-segmented; endopod of other legs one-segmented. All exopodal segments of about same length; first exopodal segment of all legs without inner seta, second with inner seta; third exopodal segment of first leg with two outer spines and no inner setae, that of second leg with three outer spines and no inner setae, third leg with two outer spines and no inner setae and fourth leg with two outer spines and one inner seta. First endopodal segment of first leg large, reaching to posterior margin of second exopodal segment, armed with short spiniform inner seta; endopod of second leg with two setae, that of third leg with three and fourth leg with two setae. Inner spine on basis of first leg transformed, smooth and inflated distally, in male; only other sexual dimorphism in swimming legs involves the outer apical seta on third leg endopod, which is much shorter and spiniform in male. Fifth legs same in both sexes, reduced to single wide cuticular plate, but distinct from somite, with all armature on two lateral knobs; inner knob, representing exopod, armed with three smooth slender setae; outer knob represents outer part of basis and armed with single seta; endopodal lobe absent. Sixth leg in male a distinct cuticular plate, without armature or ornamentation.

Type and only species. *Lucionitocrella yalleenensis* **sp. nov.**

Etymology. The genus name is dedicated to Prof Giuseppe Lucio Pesce (University of L'Aquila, Italy), as a recognition of his huge contribution to copepodology in general and especially to his pioneering work on Australian subterranean copepods. As both his home and the University of L'Aquila were completely destroyed in a recent powerful earthquake, we hope that he will find strength to continue his contribution in this field. His middle name is prefixed to the existing genus name *Nitocrella*. Gender feminine.

Lucionitocrella yalleenensis **sp. nov.**
(Figs 8–9)

Type material. Holotype, adult female dissected on one slide (WAM C37356); allotype, adult male dissected on one slide (WAM C37357); Australia, Western Australia, Pilbara region, Yalleen Station, bore MILLYARRA64A, 20 November 2003, leg. M. Scanlon and J. Cocking (DEC), 21°49'03"S 116°42'39"E.

Description. FEMALE (HOLOTYPE). Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding appendages and caudal setae), 0.421 mm. Preserved specimen colourless. Nauplius eye absent. Prosome comprising cephalothorax and three free pedigerous somites, while urosome comprising fifth pedigerous somite, genital double-somite and three abdominal somites. Habitus (Fig. 8A) cylindrical but not very slender, without distinct demarcation between prosome and urosome; prosome/urosome ratio 0.95; greatest width at third (second free) pedigerous somite. Body length/width ratio about 4.7; cephalothorax about as wide as genital double-somite. Free pedigerous somites without pronounced lateral or dorsal expansions. Integument weakly chitinized and without cuticular windows. Rostrum very small, membranous, ovoid, about as long as wide and not demarcated at base; ornamented with two dorsal sensilla.

Cephalothorax (Figs 8A–B) incorporating first prosomite, nearly cylindrical in dorsal view, about 1.2 times as long as wide; represents about 24% of total body length. Surface of cephalic shield and tergites of first three free pedigerous somites ornamented with few large sensilla; third pedigerous somite additionally with pair of dorsal cuticular pores. Hyaline fringe of all prosomites narrow and smooth. Fifth pedigerous (first urosomal) somite ornamented with four dorsal and two lateral sensilla (one on each side); hyaline fringe smooth both dorsally and laterally. Sclerotized joint (Figs 8A & C, 9A) present between fifth pedigerous and genital double somites and clearly visible both ventrally and dorsally.

Genital double-somite (Figs 8C, 9A) 0.8 times as long as wide (ventral view), without visible suture but slightly constricted ventrally at 2/5; ornamented with eight large sensilla dorsally (four at middle, four near posterior margin), two posterior ventral sensilla, two ventral cuticular pores at midlength and transverse row of small spinules between ventral sensilla; hyaline fringe completely smooth both ventrally and dorsally. Genital field with single small copulatory pore (at about proximal third of double-somite length), narrow but well sclerotized copulatory duct and two small triangular seminal receptacles. Single small genital aperture covered by fused reduced sixth legs, represents 37% of somite width. Third urosomite ornamented with six large sensilla near posterior margin (four dorsal and two ventral) and posterior ventral row of spinules; hyaline fringe smooth. Preanal somite with smooth hyaline fringe dorsally and ventrally, ornamented only with short posterior row of small spinules ventrally between two cuticular pores. Anal somite (Figs 8C, 9A–B) ornamented with pair of large dorsal sensilla, four lateral cuticular pores (two on each side) and transverse interrupted row of spinules (medial ones longest) along posterior ventral margin. Anal operculum (Fig. 9B) slightly convex, not reaching to posterior end of anal somite, represents 57% of somite's width; ornamented near its posterior margin with 26 minute spinules of significantly smaller size than spinules on posterior ventral margin of anal somite. Anal sinus smooth and widely opened.

Caudal rami (Figs 8C, 9A–B) short, slightly longer than their greatest width (ventral view), conical, slightly divergent, with space between them about one ramus width; armed with seven armature elements (three lateral, one dorsal and three apical). Ornamentation consists of two spinules at base of distal lateral seta, one dorsal cuticular pore and posterior row of four or five spinules ventrally. Dorsal seta smooth, inserted near posterior margin and close to inner margin, about twice as long as caudal ramus, triarticulate at base. Proximal

lateral seta about 0.7 times as long as dorsal one, arising somewhat dorsolaterally at about 2/5 of ramus length. Distal lateral seta smooth, arising at 3/4 of ramus length, 0.8 times as long as dorsal one. Inner apical seta smooth, about as long as ramus. Middle apical seta strongest, broken along breaking plane on both rami. Outer apical seta with breaking plane, ornamented with spinules on both margins.

Antennula (Fig. 9C) eight-segmented, unornamented, slender, slightly longer than cephalothorax. Strong aesthetasc on fourth segment reaches beyond tip of appendage for length of last segment; much more slender apical aesthetasc on eighth segment fused basally with two apical setae. Setal formula: 1.8.6.3.2.2.4.7. All setae smooth, except for unipinnate seta on first segment, without breaking plane and uniarticulate at base. Length ratio of antennular segments, from proximal end and along caudal margin, 1 : 1.8 : 1 : 1.2 : 0.6 : 0.8 : 0.6 : 0.9.

Antenna (Fig. 9D) composed of coxa, basis, two-segmented endopod and one-segmented exopod. Coxa very short, unarmed and unornamented. Basis three times as long as coxa, about 1.3 times as long as wide, unornamented and unarmed. First endopodal segment about 1.8 times as long as wide and 1.3 times as long as basis, unornamented and unarmed. Second endopodal segment longest, 1.5 times as long as first and 2.8 times as long as wide, armed medially at 2/3 with two smooth spines flanking thin seta; apical armature consisting of five geniculate setae, longest one fused basally to additional smaller seta bearing proximal tuft of fine setules; ornamentation consists of few spinules along anterior surface. Exopod one-segmented, very small, 0.3 times as long as basis and 2.2 times as long as wide, unornamented but armed with single unipinnate seta, which 4.3 times as long as exopod.

Labrum (Fig. 9E) not very large compared with cephalothorax, trapezoidal, rigidly sclerotized, with relatively narrow and convex cutting edge; ornamented with one apical row of small spinules in between two subapical rows of strong spinules (seven on each side). Two small ellipsoid fields of gustatory papillae visible on dorsal (posterior) surface.

Paragnaths (Fig. 9F) ovoid, fused basally into bilobate labium; each ornamented with apical row of large spinules, one spinule on outer margin and longitudinal row of four large curved spinules at middle, close to inner margin, which continues into row of small spinules that almost reaches to apical margin, as well as some minute apical spinules on interlobal plate.

Mandibula (Figs 9G–H) with narrow cutting edge on elongated coxa, armed with coarser teeth at ventral half, finer teeth at dorsal half and one unipinnate seta dorsally. Palp very small, uniramous, comprising basis and one-segmented endopod. Basis unarmed and unornamented, 2.3 times as long as wide. Endopod also slender and unornamented, about as long as basis but somewhat wider at distal part; armed apically with five slender smooth setae.

Maxillula (Fig. 9I) with large praecoxa; arthrite rectangular, not movable, unornamented but armed with two smooth setae on anterior surface, three short setae on dorsal margin and four apical elements (probably three spines and one seta). Coxal endite armed apically with one pinnate, strong and recurved seta dorsally and two smooth slender setae ventrally, all of about same length. Basis somewhat shorter than coxal endite, armed with four smooth setae apically and one smooth seta subapically. Endopod a minute but distinct segment, armed apically with single smooth seta.

Maxilla (Fig. 9J) with proximal syncoxal endite absent; distal endite well developed, highly mobile, armed with one curved bipinnate spine and two smooth subequal setae, which 1.4 times as long as spine. Basis drawn out into long and nearly straight claw, with shorter spiniform curved seta at its base; no cuticular pore or other ornamentation observed. Endopod represented by minute segment, armed with two smooth subequal, long apical setae.

Maxilliped (Fig. 9K) with well developed syncoxa ornamented with several minute spinules near inner distal corner and armed with single smooth seta subapically, 1.5 times as long as wide. Basis twice as long as wide and almost 1.4 times as long as syncoxa, unarmed and unornamented. Endopod represented by long and slightly curved claw, ornamented distally with row of spinules along concave side; with thin seta at base.

All swimming legs with three-segmented exopod; endopod of first leg three-segmented (Fig. 8D), endopod of other legs one-segmented (Figs 8E–G). Armature formula of swimming legs as follows (inner/

outer element; inner/terminal/outer element):

	Exopod			Endopod		
Segments	1	2	3	1	2	3
First leg	0/1	1/1	0/2/2	1/0	0/0	1/1/1
Second leg	0/1	1/1	0/2/3	1/1/0	-	-
Third leg	0/1	1/1	0/2/2	1/2/0	-	-
Fourth leg	0/1	1/1	1/2/2	1/1/0	-	-

Intercoxal sclerite of all swimming legs with concave distal margin and without surface ornamentation. Praecoxae of all legs very short and unornamented. Coxa of third swimming leg ornamented with several minute spinules on anterior surface, that of other legs unornamented; all coxae unarmed. Basis of each leg ornamented with row of spinules near outer margin, that of first leg also with posterior row between rami and several small spinules near inner margin; first and second legs armed with short smooth spine, third and fourth legs with slender seta on outer margin (longest one on third leg); first leg with short stout spine on inner distal corner. All exopodal and endopodal segments ornamented with strong spinules along outer margin; some segments also with spinules along inner distal margin. All exopodal segments of about same length. First swimming leg (Fig. 8D) with first endopodal segment about three times as long as wide and almost reaching to distal margin of second exopodal segment; endopod longer than exopod, reaching beyond distal margin of exopod for length of last endopodal segment. Endopod of second and third swimming legs (Figs 8E–F) as long as first exopodal segment; endopod of fourth swimming leg (Fig. 8G) half as long as first exopodal segment. Apical armature element(s) on first leg geniculate, pinnate on outer (concave) side and either plumose (innermost one on exopod) or smooth (all others) on inner side. Third exopodal segment of other legs with plumose inner apical seta and heterogeneously ornamented outer apical seta (plumose on inner margin, pinnate on outer; transitional stage between seta and spine). Inner element on second exopodal segment short and spiniform, while all outer exopodal spines strong and bipinnate. Apical endopodal element(s) of second to fourth legs slender and plumose, more than three times as long as segment, while inner seta short, bipinnate and spiniform.

Fifth legs (Figs 8C & H, 9A) fused completely together into single distinct plate, with each leg represented by two unornamented but armed lateral knobs. Inner knob, representing exopod, armed with three smooth slender setae, innermost one longest, outermost shortest. Outer knob represents outer basal part and armed with single long smooth seta; this seta much longer than any seta on inner knob. Endopodal lobe reduced to simple hyaline fringe, unarmed and unornamented.

Sixth legs (Fig. 8C) completely fused together, indistinct, forming simple operculum covering single gonopore, without ornamentation but each armed with single minute seta.

MALE (ALLOTYPE). Body length 0.418 mm. Habitus, ornamentation of prosomites, rostrum, colour and nauplius eye similar to female. Hyaline fringe of all prosomites smooth and no cuticular windows observed.

Genital somite more than twice as wide as long. Single small, longitudinally placed spermatophore visible inside fifth pedigerous and genital somite (Fig. 9L). Urosomite ornamentation similar to female, although genital somite with one additional lateral sensillum and preanal somite with longer ventral row of smaller spinules.

Anal somite and caudal rami (Fig. 9L) proportions, armature and ornamentation very similar to female.

Antennula (Fig. 9M) long and slender, ten-segmented, not strongly geniculate, with geniculation between seventh and eighth segments, unornamented. Very long and broad aesthetasc present on apical acrothek of fifth segment (homologous to aesthetasc on fourth segment in female); one smaller aesthetasc on tenth segment fused basally to two apical setae. First two and last two segments similar to female. Setal formula: 1.10.6.1.6.1.2.1.4.7. Most setae smooth and slender; all setae without breaking plane; two setae on fifth segment and one each on sixth and seventh very short and unipinnate. Just four lateral setae on tenth segment and one seta on ninth segment biarticulating on basal part; all other setae uniarticulate.

FIGURE 8. *Lucionitocrella yalleenensis* **gen. et sp. nov.**, holotype female: A—habitus, dorsal view; B—cephalothorax, lateral view; C—urosome, ventral view; D—first swimming leg; E—second swimming leg; F—third swimming leg; G—fourth swimming leg; H—right fifth leg. Scales = 0.1 mm.

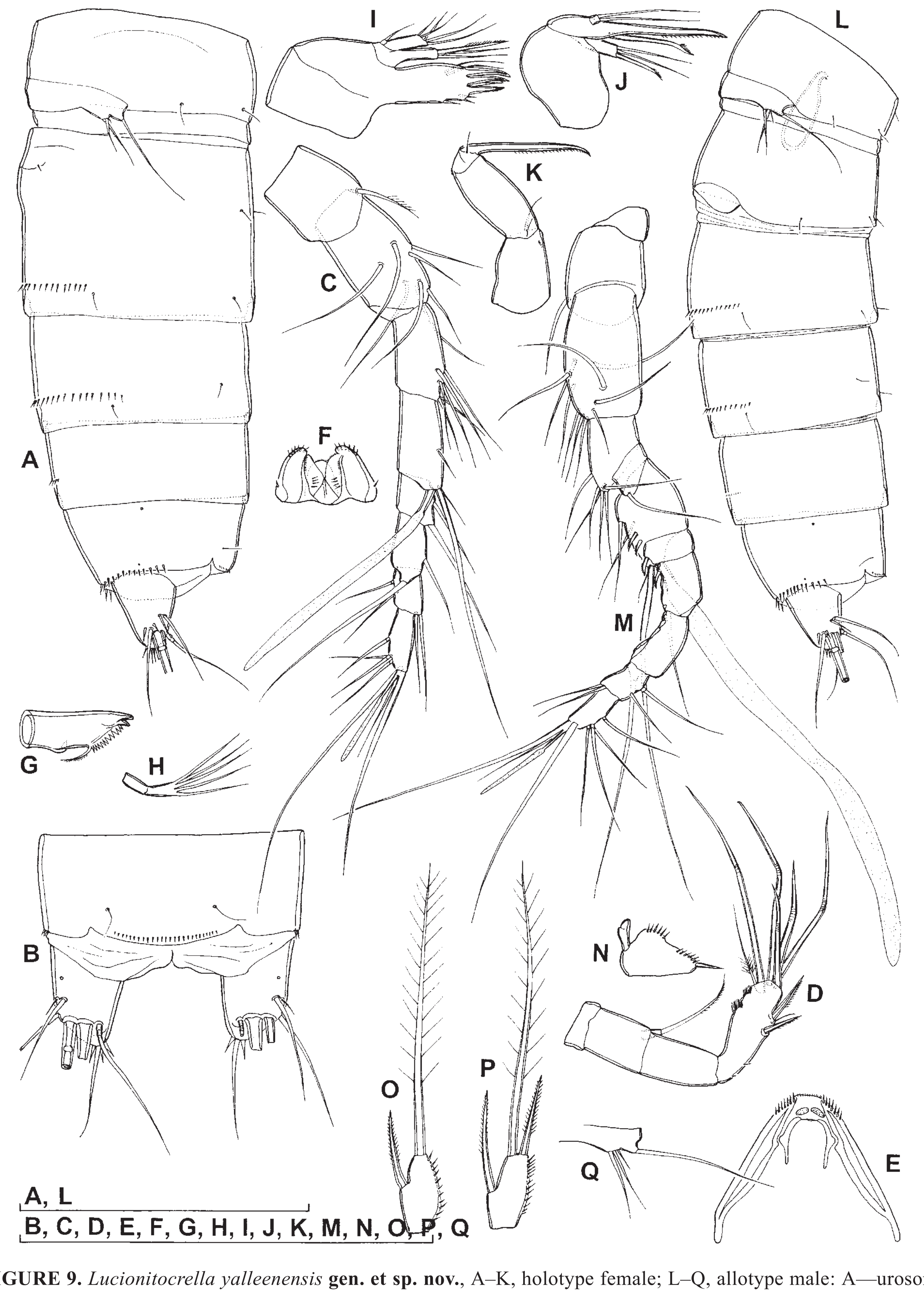

FIGURE 9. *Lucionitocrella yalleenensis* **gen. et sp. nov.**, A–K, holotype female; L–Q, allotype male: A—urosome, lateral view; B—anal somite and caudal rami, dorsal view; C—antennula; D—antenna; E—labrum; F—paragnaths; G—cutting edge of mandibula; H—mandibular palp; I—maxillula; J—maxilla; K—maxilliped; L—urosome, lateral view; M—antennula; N—basis of first swimming leg; O—endopod of second swimming leg; P—endopod of third swimming leg; Q—left fifth leg. Scales = 0.1 mm.

Antenna, labrum, paragnaths, mandibula, maxillula, maxilla, maxilliped, second swimming leg (Fig. 9O) and fourth swimming leg very similar to female.

First swimming leg (Fig. 9N) with inner spine on basis significantly modified, smooth and inflated distally.

Third swimming leg (Fig. 9P) with outer apical element on endopod spiniform and bipinnate (not plumose) and much shorter than in female.

Fifth leg (Figs 9L & Q) remarkably similar to female, except middle seta somewhat longer and exopodal lobe less pronounced.

Sixth legs (Fig. 9L) not fused medially together, distinct from somite, represented by slightly asymmetrical ellipsoid cuticular plates without armature or ornamentation.

Variability. No important asymmetries or variablities were observed between the one male and one female collected and studied (other than sexually dimorphic characters).

Etymology. The species is named after the type locality, Yalleen Station, with the addition of the Latin suffix for place "-*ensis*". The specific name consequently is an adjective for place.

Remarks. As mentioned in the Remarks section for the previous species, *Lucionitocrella yalleenensis* **gen. et sp. nov.** differs from all other *Stygonitocrella s. l.* members by the plesiomorphic three outer armature elements of the third exopodal segment of the second leg. Other plesiomorphic features include the presence of an inner apical seta on the ultimate endopodal segment of the third leg (Table 2, character 37), as well as distal inner seta on the endopod of the fourth leg (character 46), which it shares only with the Mexican *Eduardonitocrella mexicana* (Suárez-Morales & Iliffe, 2005) comb. nov. (see *S. mexicana* in Table 2). However, the two species are not closely related and we have previously explained the nonhomologous nature of their endopodal armature elements of the third leg in the Remarks section for *Gordanitocrella trajani* **gen. et sp. nov.** (see above). The two species also differ in many other characters, including their armature pattern on the endopodal segment of the second and fourth legs (characters 26, 27, 28, 43, 44 & 46 in Tables 1 & 2), anal operculum (plesiomorphic in *E. mexicana*), as well as reductions in the antennula, mandibula, maxilla and maxilliped in *E. mexicana* and in the antenna in *L. yalleenensis.*

In the species included in this study, an antennal exopod with only 1 seta was observed only in *L. yalleenensis* and *Inermipes humphreysi* Lee & Huys, 2002, but it also occurs in the completely unrelated *Abnitocrella halsei* Karanovic, 2006 (see Karanovic, 2006), and some other taxa. It is interesting to note that while the armature of the fifth leg in *L. yalleenensis* is quite reduced, the leg itself is not fused to the somite. Thus, superficially similar fifth legs that are highly reduced in the genera *Abnitocrella* Karanovic, 2006, *Kimberleynitocrella* **gen. nov.** and *Lucionitocrella* **gen. nov.** are in fact very different when examined more closely and especially when considering homologous armature elements and the nature and extent of reductions in their segmentation. However, closely related species in this branch of freshwater ameirids with differently reduced fifth legs indicated to us that this character (or this group of characters) is less relevant for reconstructing their phylogenetic relationships. That is why those characters were weighted less in our cladistic analysis. It seems that *Lucionitocrella* has no obvious autapomorphic features (or they are masked with homoplastic characters in other members), and it is placed on the cladogram as a sister group to all other *Stygonitocrella s. l.* species, except *Kimberleynitocrella* and *Gordanitocrella* **gen. nov.** The genus is well defined by a combination of plesiomorphic and apomorphic features.

Genus *Stygonitocrella* Reid, Hunt & Stanley, 2003

Diagnosis emended. Small to medium sized Ameiridae, with cylindrical habitus and no distinct demarcation between prosome and urosome. Integument weakly chitinized, with or without cuticular windows on prosomites; hyaline fringe of prosomites smooth, those of urosomites smooth or finely serrated. First pedigerous somite incorporated into cephalothorax. Prosome weakly ornamented with moderately large sensilla, urosome additionally ornamented with ventral posterior rows of small spinules. Genital somite free

or fused with first abdominal in double-somite; genital field with single large copulatory pore, wide copulatory duct and two small semicircular seminal receptacles; single small genital aperture covered by fused reduced sixth legs. Anal operculum wide and convex, reaching to posterior end of anal somite, smooth or ornamented with small spinules near posterior margin. Caudal rami from one to five times as long as their greatest width and slightly divergent; armed with seven armature elements (three lateral, one dorsal and three apical), all positioned at posterior end. Antennula long and slender, eight-segmented in female and ten-segmented and geniculate in male; with one seta on first segment. Antenna composed of coxa, basis, two-segmented endopod and one-segmented exopod; exopod armed with two or three setae. Mandibula with narrow cutting edge and two-segmented palp; basis armed with single seta, endopod with three to five apical setae. Maxillular endopod with one apical seta. Maxilla with two endites on syncoxa; endopod minute, armed with two slender setae. Maxilliped three-segmented, with or without seta on syncoxa and without seta on endopod. All swimming legs with three-segmented exopod. Endopod of first leg three-segmented; endopod of second and third swimming legs one- or two-segmented, while endopod of fourth swimming leg always one-segmented. All exopodal segments of about same length; first exopodal segment of all legs without inner seta, second with; third exopodal segment of all swimming legs with two outer spines, that of first leg without inner setae, second and third leg without inner setae (except for *S. orghidani* Petkovski, 1973) and fourth leg with one or two inner setae. First endopodal segment of first leg large, at least as long as first two exopodal segments combined, with or without inner seta; apical endopodal segment of second, third and fourth legs armed with long apical seta. Basis of first leg in male with transformed inner spine; no other sexual dimorphism in swimming legs. Fifth legs similar in both sexes, variously reduced but always distinct from somite, with three elements on baseoendopod and maximum of four on exopod. Sixth legs in male armed with two setae maximum.

Type species. *Stygonitocrella montana* (Noodt, 1965) [= *Nitocrella montana* Noodt, 1965].

Other species. *Stygonitocrella dubia* (Chappuis, 1937) [= *Nitocrella* dubia Chappuis, 1937]; *Stygonitocrela guadalfensis* Rouch, 1985; and *Stygonitocrella sequoyahi* Reid, Hunt & Stanley, 2003.

Incertae sedis. *Stygonitocrella orghidani* (Petkovski, 1973) [= *Nitocrella orghidani* Petkovski, 1973].

Synonymy. *Fiersiella* Huys, 2009.

Remarks. As mentioned in the Introduction section, while describing this genus Petkovski (1976) did not designate a type species, which according to the ICZN (Article 13.3) means that this name was unavailable. In order to be available every new genus-group name published after 1930 must be accompanied by the fixation of a type species, in addition to satisfying the provisions of Article 13.1, i.e. providing or citing a description or definition of the genus. Reid *et al.* (2003) designated the South American *Stygonitocrella montana* (Noodt, 1965) as the type species of the genus *Stygonitocrella* Reid, Hunt & Stanley, 2003 and gave a revised diagnosis, making the generic name available with their authorship. This was accepted by Lee & Huys (2002), Karanovic (2006) and Wells (2007), although Suárez-Morales & Iliffe (2005) continued to attribute authorship to Petkovski (1976). Unfortunately, Reid *et al.* (2003) also treated all previously described species as new combinations and cited all author names in parentheses. Although, neither Article 11.9.3 nor Article 51.3 specifically addresses this case, it remains unclear as to whether the name of the author of a species that was assigned originally to an unavailable genus is designated in parentheses, after the same genus name has become available under different authorship. This is not a case of a generic name being different from the original one, since the author attribution does not form part of a name in zoological nomenclature (Article 51.1). Therefore, we think parentheses should not be used and it is at least an overstatement to refer to such cases as new combinations.

Suárez-Morales & Iliffe (2005) also proposed the subdivision of *Stygonitocrella* into two subgenera, *Eustygonitocrella* Suárez-Morales & Iliffe, 2005 and *Fiersiella* Suárez-Morales & Iliffe, 2005, based on the condition of the female fifth leg baseoendopod. As we can see in the cladisitic analysis in this paper, characters of the fifth leg have very little importance at the generic (or subgeneric level), as they can be very different in some obviously closely related species (*Megastygonitocrella pagusregalis* **sp. nov.** and *Megastygonitocrella kryptos* **sp. nov.** for example—see below), but can also be superficially similar in

different genera (see the Remarks section for *Lucionitocrella yalleenensis* **gen. et sp. nov.**). We think their subdivision of the genus is not taxonomically sound and by definition excludes those species that are known just as males, although Suárez-Morales & Iliffe (2005) included *Stygonitocrella dubia* (Chappuis, 1937), for which females are still unknown. Also, their revision suffers from some serious nomenclatural problems. As Wells (2007) pointed out, *Eustygonitocrella* is obviously an objective synonym of *Stygonitocrella,* since it contains the type species *S. montana*, and must, therefore, be relegated to a junior synonym of the nominotypical subgenus (ICZN Article 44.1). For the subgenus *Fiersiella*, the authors designated *S. dubia* as "... the representative species ...", without following the rules of the ICZN (Article 67.5), making this genus-group name unavailable. According to the provisions of the Code, type designation must be rigidly constructed by using the term "type species" (or an equivalent term in another language) to avoid ambiguity. Huys (2009) made the subgeneric name available by fixing *Stygonitocrella sequoyahi* Reid, Hunt & Stanley, 2003 as the type species. Unfortunately, as our cladistic analysis shows, both *S. dubia* and *S. sequoyahi* belong to the same clade as the type species of *Stygonitocrella*, and consequently, *Fiersiella* Huys, 2009 is considered here as a subjective junior synonym of the former.

The genus *Stygonitocrella*, as redefined here, contains only four species: *S. montana* from Argentina, *S. sequoyahi* from the United States of America and *S. dubia* and *S. guadalfensis* Rouch, 1985 from Spain (see Chappuis 1937; Noodt 1965; Rouch 1985; Reid *et al.* 2003). Reid *et al.* (2003) pointed out that the generic placement of *Stygonitocrella orghidani* (Petkovski, 1973) is questionable and Lee & Huys (2002) formally placed it as *incertae sedis* in the wider defined genus *Stygonitocrella*. As noted both by Lee & Huys (2002) and Reid *et al.* (2003), the description of this Cuban species by Petkovski (1973) is not sufficient for modern taxonomic standards and we also include it here in the redefined genus *Stygonitocrella* as *incertae sedis* solely on the basis of the endopodal armature of the swimming legs, although it does not cluster with this group of freshwater ameirids. Unfortunately, the type material of this species no longer exists (T. Petkovski pers. comm.) and any further taxonomic decision would have to await study of newly collected topotypes.

The main character that defines *Stygonitocrella* is the armature formula of the ultimate endopodal segment of the second to fourth swimming legs, which is 1.1.1 and is not found in any other group studied here. The five taxa included herein in this genus are united by the loss of the outer subapical spine of the third leg endopod (Table 2, character 35). This feature is convergently exhibited in three other genera: *Gordanitocrella* **gen. nov.**, *Lucionitocrella* **gen. nov.** and *Psammonitocrella* Huys, 2009. The first two genera are discussed above and are not closely related to *Stygonitocrella,* as they each have a greater number of plesiomorphic characters in their swimming legs, but more reduced mouth appendages and antenna. The genus *Psammonitocrella* is very well defined by a number of autapomorphic features, such as its unusually reduced exopodal armature of the swimming legs and the absence of a transformed inner basal spine of the male first leg, as well as some other unusual reductions (see below). However, it is not so hard to imagine the ancestor of *Psammonitocrella* being morphologically quite similar to *S. sequoyahi,* and it is interesting to note that both species of *Psammonitocrella* and *S. sequoyahi* live in North America and have unusually elongated caudal rami.

The only armature element on the ultimate endopodal segment of the second leg in *Stygonitocrella* is probably the ancestral inner apical seta (just as in the third leg), but this is not so easy to confirm with less than perfect drawings of some members of the genus. The nature of the only armature element on the fourth leg endopod is also not so clear, but we believe it to be the ancestral outer subapical spine, as in the genus *Megastygonitocrella* **gen. nov.** (see below). The mouth appendages are described only for two species in this genus (*S. sequoyahi* and *S. guadalfensis*), but interestingly both have some unusual plesiomorphic characters, like the presence of a mandibular basal seta (only present in one other species studied here, i.e. *M. karamani* (Petkovski, 1959)) and two endites on the maxillar syncoxa (also reported for *S. montana*). Unfortunately, many earlier species descriptions in this group of freshwater ameirids lack some or most data on mouth appendages (see Table 2).

Key to species of *Stygonitocrella*.

1	Caudal rami shorter than anal somite	2
-	Caudal rami longer than anal somite	*S. sequoyahi* Reid, Hunt & Stanley, 2003
2	Armature on fifth leg endopod absent	3
-	This armature present	*S. dubia* (Chappuis, 1937)
3	Antennal exopod with three setae	4
-	Only two setae present	*S. orghidani* (Petkovski, 1973)
4	Anal operculum smooth	*S. montana* (Noodt, 1965)
-	Operculum ornamented	*S. guadalfensis* Rouch, 1985

Genus *Reidnitocrella* gen. nov.

Diagnosis. Medium sized Ameiridae, with cylindrical habitus and no distinct demarcation between prosome and urosome. Integument weakly chitinized and without cuticular windows; hyaline fringe of all somites smooth. First pedigerous somite incorporated into cephalothorax. Prosome weakly ornamented with moderately large sensilla, urosome with or without ventral posterior rows of small spinules. Genital double-somite with visible suture laterally and dorsally; genital field with single large copulatory pore, wide copulatory duct and two small semicircular seminal receptacles; single small genital aperture covered by fused reduced sixth legs. Anal operculum narrow and convex, not reaching to posterior end of anal somite, unornamented. Caudal rami ovoid or cylindrical, 1.5 times as long as their greatest width and slightly divergent; dorsal seta inserted near posterior margin and very close to inner margin, about twice as long as ramus; proximal lateral seta arising somewhat dorsolaterally at middle; distal lateral seta arising at 5/6 and laterally; inner apical seta small; principal apical setae bipinnate, with breaking plane. Antennula long and slender, eight-segmented in female and ten-segmented and not strongly geniculate in male; with seta on first segment. Antenna composed of coxa, basis, two-segmented endopod and one-segmented exopod; exopod armed with three setae. Mandibula with two-segmented palp; basis unarmed, endopod with four apical setae. All swimming legs with three-segmented exopod. Endopod of first leg three-segmented, while that of second leg two-segmented, third leg one- or two-segmented and fourth leg always one-segmented. All exopodal segments of about same length; first exopodal segment of all legs without inner seta, second with; third exopodal segment of all legs with two outer spines, that of first, second and third legs without inner setae, that of fourth leg with two inner setae. First endopodal segment of first leg large, armed with one inner seta; subapical endopodal segment of second and third legs (when present) armed with one inner seta or unarmed; apical endopodal segment of second leg armed with one inner seta and one apical plumose seta, that of third leg with inner apical plumose seta and outer apical plumose spine, while endopod of fourth leg armed with single apical spine. Basis of first leg in male with transformed inner spine. Fifth leg same in both sexes, biramous but with baseoendopods fused both medially together and to somite; endopodal lobe not recognizable and without armature or ornamentation; basal outer seta arising from very long setophore; exopod a distinct segment, quadriform, small, armed with two or three slender smooth setae.

Type species. *Reidnitocrella tianschanica* (Borutzky, 1972) comb. nov. [= *Nitocrella tianschanica* Borutzky, 1972: p.111, figs 7/1–7/10].

Other species. *Reidnitocrella borutzkyi* **sp. nov.** [= *Nitocrella tianschanica* Borutzky, 1972: p. 111, figs 7/11–7/16]; *Reidnitocrella pseudotiaschanica* (Sterba, 1973) comb. nov. [= *Nitocrella pseudotianschanica* Sterba, 1973]; *Reidnitocrella djirgalanica* (Borutzky, 1978) comb. nov. [= *Nitocrella djirgalanica* Borutzky, 1978].

Etymology. The new genus is named in honour to Dr Janet W. Reid (University of Virginia, USA), as recognition of her enormous contribution in the field of freshwater copepod taxonomy. She (with two other colleagues) also made the genus name *Stygonitocrella* Reid, Hunt & Stanley, 2003 available, by designating the type species. Her surname is prefixed to the existing genus name *Nitocrella*. Gender feminine.

Remarks. Species of the genus *Reidnitocrella* **gen. nov.** form a well supported clade on the cladogram (Fig. 18) of this group of freshwater ameirids (*Stygonitocrella s. l.*) and, interestingly, all come from a relatively small area in central Asia. *Reidnitocrella pseudotianschanica* (Sterba, 1973) was described from central Afghanistan, while *R. tianschanica* (Borutzky, 1972), *R. djirgalanica* (Borutzky, 1978) and *R. borutzkyi* **sp. nov.** all come from the interstitial of Lake Issyk-Kul in Kyrgyzstan (see Borutzky 1972, 1978; Sterba 1973).

Their armature formula of the ultimate endopodal segment of the second to fourth legs is either 2.2.1 or 2.1.1, as is the endopodal segmentation formula of the same legs. But it is the nature of these elements that is of far more importance. While two armature elements on the ultimate endopodal segment of the second leg is also found in *Eduardonitocrella mexicana* (Suárez-Morales & Iliffe, 2005) comb. nov., *Neonitocrella insularis* (Miura, 1962) and *Megastygnitocrella karamani* (Petkovski, 1959) comb. nov., they represent the ancestral two apical setae in *E. mexicana* (Table 2, characters 26 & 27), the outer subapical spine and outer apical seta in *N. insularis* and *M. karamani* (characters 25 & 26) and the ancestral outer apical and distal inner setae in the genus *Reidnitocrella* (characters 26 & 28). In fact, the nature of these elements in *Reidnitocrella* is the same in only two other species: *Gordanitocrella trajani* **sp. nov.** and *Lucionitocrella yalleenensis* **sp. nov.** As we discussed above, these two species have a number of unique plesiomorphic characters (and some autapomorphic) and are not closely related to any of the recent *Stygonitocrella s. l.* species. If, for example, we just compare the armature elements on the endopod of the third leg, it becomes clear that those of *Gordanitocrella* **gen. nov.** represent characters 36, 38 & 39, while those of *Lucionitocrella* **gen. nov.** represent characters 36, 37 & 39 and of *Reidnitocrella* characters 35 & 36.

On the other hand, the nature of the armature elements on the ultimate endopodal segment of the third and fourth legs is exactly the same in *Reidnitocrella* **gen. nov.** and *Megastygonitocrella* **gen. nov.**, which suggests that these two genera are probably most closely related. However, all *Megastygonitocrella* species have the ancestral outer subapical spine on the endopod of the second leg (character 25) present (absent in *Reidnitocrella*) and in all species, except in *M. karamani* (Petkovski, 1959), this is also the only armature element. Also all *Megastygonitocrella* species have lost the inner seta on the second exopodal segment of the first leg (character 17), while it is present in all four *Reidnitocrella* species. Unfortunately, the mouth appendages are practically unknown for all four representatives of the latter genus, so many potentially valuable characters could not be included in the cladistic analysis.

Key to species of *Reidnitocrella* gen. nov.

1 Endopod of third leg with two armature elements 2
- Endopod of third leg with only one element.......... *R. djirgalanica* (Borutzky, 1978)
2 Endopod of third leg one-segmented 3
- Endopod of third leg two-segmented .... *R. borutzkyi* **sp. nov.**
3 Exopod of fifth leg with three setae .... *R. tianschanica* (Borutzky, 1972)
- Exopod of fifth leg with two setae.......... *R. pseudotianschanica* (Sterba, 1973)

Reidnitocrella borutzkyi sp. nov.

Synonymy. *Nitocrella tianschanica* **sp. nov.** [partim.] – Borutzky 1972: p. 111, figs 7/11–7/16.
[non] *Nitocrella tianschanica* **sp. nov.** – Borutzky 1972: p. 111, figs 7/1–7/15.

Type material (not examined). Holotype, adult female dissected on one slide (Borutzky, 1972) from a well (sample no 9) near the Biological Station in Cholpon-Ata city, 1,606 m a.s. l., Lake Issyk-Kul, Kyrgyzstan, 11 July 1961, leg. A. Yankovskaya & T. Kac, 42°05'N 77°05'E.

Other material (also not examined). Three adult males (one dissected on one slide; Borutzky 1972) from interstitial of Lake Issyk-Kul (Karaman-Chappuis pit no 16; sample no 34), near the Biological Station

in Cholpon-Ata city, 1,606 m a.s.l., Kyrgyzstan, 14 August 1961, leg. A. Yankovskaya & T. Kac, 42°05'N 77°05'E.

Redescription. FEMALE (HOLOTYPE). Total body length more than 0.5 mm. Habitus cylindrical, slender, without distinct demarcation between prosome and urosome. Free pedigerous somites without pronounced lateral or dorsal expansions. Integument not strongly chitinized and without cuticular windows. Cephalothorax with completely incorporated first pedigerous somite. Surface of cephalic shield and tergites of three free pedigerous somites ornamented only with large sensilla. Hyaline fringe of all prosomites narrow and smooth. Genital double-somite without visible suture and only slightly wider at anterior part; hyaline fringe finely serrated both ventrally and dorsally. Genital field with single large copulatory pore, sclerotized wide copulatory duct and two small seminal receptacles. Single small genital aperture covered by fused reduced sixth legs, represents 70% of somite width. Third and fourth free urosomites without rows of small spinules. Anal somite ornamented with pair of large dorsal sensilla and posterior ventral row of spinules, those near inner corner of caudal rami especially large. Anal operculum small and convex, unornamented, not reaching to posterior end of anal somite, represents 50% of somite's width. Anal sinus smooth.

Caudal rami short and cylindical, clearly convergent, with space between them more than one ramus width, about twice as long as wide; armed with seven armature elements (three lateral, one dorsal and three apical). Ornamentation consists of several spinules at base of dorsal and distal lateral seta. Dorsal seta smooth, inserted posteriorly and close to inner margin, 1.8 times as long as caudal ramus, probably biarticulate at its base. Proximal and distal lateral setae smooth and of about same length as dorsal seta; proximal seta arising somewhat dorsolaterally at midlength; distal lateral seta arising close to posterior margin. Inner apical seta smooth, about 1.4 times as long as ramus. Both principal setae bipinnate; inner one twice as long as outer principal seta.

Antennula eight-segmented, slender. Long and relatively slender aesthetasc on fourth segment reaches beyond tip of appendage for length of last two segments combined and fused basally with large subapical seta; much smaller and even more slender apical aesthetasc on eighth segment fused basally to two apical setae. Seta on first segment unipinnate, all other setae smooth.

Antenna composed of coxa, basis, two-segmented endopod and one-segmented exopod. Exopod small, armed with three setae.

Labrum and paragnaths unknown.

Mandibula with uniramous palp, comprising basis and one-segmented endopod. Basis unarmed and unornamented, 1.5 times as long as wide and 1.2 times as long as endopod. Endopod slender and unornamented, about twice as long as wide, armed with four slender and smooth apical setae.

Maxillula, maxilla and maxilliped unknown.

All swimming legs with three-segmented exopod; endopod of first leg three-segmented, that of second and third legs two-segmented, while endopod of fourth swimming leg one-segmented. Armature formula of swimming legs as follows (inner/outer element; inner/terminal/outer element):

	Exopod			Endopod		
Segments	1	2	3	1	2	3
First leg	0/1	1/1	0/2/2	1/0	0/0	1/1/1
Second leg	0/1	1/1	0/2/2	1/0	1/1/0	-
Third leg	0/1	1/1	0/2/2	0/0	1/1/0	-
Fourth leg	0/1	1/1	2/2/2	0/1/0	-	-

Basis of each leg armed with outer spine or seta. All exopodal and endopodal segments ornamented with strong spinules along outer margin and on outer distal corner. All exopodal segments of about same length. First endopodal segment of first swimming leg large, about 2.4 times as long as wide and about as long as first two exopodal segments combined; endopod significantly longer than exopod. Endopod of second and third swimming legs reaching to midlength of second exopodal segment, while that of fourth leg half as long as first exopodal segment. All setae on each ramus (except minute inner seta on third endopodal segment of first leg) strong and some also spiniform. Apical armature element(s) on first leg geniculate.

Fifth leg biramous but baseoendopod fused medially together and to somite. Endopodal lobe not recognizable, without armature or ornamentation. Basal outer seta slender and smooth, arising from very long setophore. Exopod a distinct segment, quadriform, small, 1.5 times as long as its maximum width, unornamented and armed with three slender smooth setae; length ratio of exopodal setae slightly different between left and right legs, although all setae on each side of similar length and longer than segment.

Sixth legs completely fused together, indistinct, forming simple operculum covering single gonopore, without ornamentation but each armed with single minute seta.

MALE FROM SAMPLE 34. Habitus, ornamentation of prosomites and caudal rami similar to female. Hyaline fringe of all somites smooth.

Antennula strongly geniculate, with geniculation between seventh and eighth segments, unornamented. Very long and broad aesthetasc present on apical acrothek of fifth segment (homologous to aesthetasc on fourth segment in female).

Antenna, labrum, mandibula, maxillula, maxilla, maxilliped, second swimming leg, and fourth swimming leg similar to female.

First swimming leg with inner spine on basis modified, inflated distally.

Third swimming leg with first endopodal segment armed with inner seta and second segment with significantly shorter inner apical seta than in female.

Fifth leg similar to female.

Sixth legs unknown.

Variability. The first endopodal segment of the third swimming leg can be with or without an inner seta, but at present this is known only as sexual dimorphism.

Etymology. The species name is dedicated to late Dr E.V. Borutzky, who first described these specimens as part of normal interspecific variability of *Nitocrella tianschanica* Borutzky, 1972. The name is a noun in the genitive singular.

Remarks. *Reidnitocrella borutzkyi* **sp. nov.** differs from *Reidnitocrella tianschanica* (Borutzky, 1972) comb. nov., in its larger size, naked abdominal somites, two-segmented endopod of the third leg, armed penultimate endopodal segment of the second leg and shorter innermost seta on the fifth leg exopod. Borutzky (1972) noted that (translated from Russian) "The female specimen from the well near the Biological station (sample no 9) somewhat differs from the above described by its larger size and a narrower fifth leg exopod.", but did not recognize it as a separate species. Given the differences observed and considering the fact that all the specimens studied by Borutzky (1972) come from a very small area, it is quite clear that he was dealing with at least two different species of *Stygonitocrella s. l.,* but was confused by their very similar (quite reduced) fifth legs. Unfortunately his descriptions lack many details, especially in the mouth appendages, so it is not possible to compare them more closely.

The new species differs from *Reidnitocrella djirgalanica* (Borutzky 1978) comb. nov. by having two armature elements on the ultimate endopodal segment of the third leg (only one in *R. djirgalanica*), like the other two species in this genus, but also by having a distinct exopodal segment of the fifth leg (the fifth leg is apparently absent in *R. djirgalanica*). Unfortunately, the description of *R. djirgalanica* is also incomplete and lacks drawings (Borutzky 1978). The new species differs from *Reidnitocrella pseudotianschanica* (Sterba, 1973) comb. nov. by its two-segmented endopod of the third leg (one-segmented in *R. pseudotianschanica*), having three setae on the fifth leg exopod (only two in *R. pseudotianschanica*) and by other small details in the ornamentation of the abdominal somites and caudal rami (see Sterba 1973).

Genus *Inermipes* Lee & Huys, 2002

Diagnosis emended. Relatively large and not very slender Ameiridae, with cylindrical habitus and no distinct demarcation between prosome and urosome, although body constricted at first urosomite. Integument weakly chitinized and without cuticular windows; hyaline fringe of all somites smooth. First pedigerous somite

incorporated into cephalothorax. Prosome weakly ornamented with very large sensilla, urosome additionally ornamented with ventral rows of spinules. Genital double-somite without visible suture but slightly constricted laterally; genital field with single large copulatory pore, wide and extremely short copulatory duct and two semicircular seminal receptacles; single small genital aperture covered by fused reduced sixth legs, without armature or ornamentation. Anal operculum wide and convex, not reaching to posterior end of anal somite, ornamented with many more spinules near posterior margin. Caudal rami conical, as long as greatest width and slightly divergent; dorsal seta inserted near posterior margin and very close to inner margin, about twice as long as ramus; proximal lateral seta arising somewhat dorsolaterally at middle; distal lateral seta arising at 5/6 and laterally; inner apical seta smaller than ramus; principal apical setae pinnate, with breaking plane. Antennula long and slender, eight-segmented in female and ten-segmented but not strongly geniculate in male; without seta on first segment. Antenna composed of coxa, basis, two-segmented endopod and one-segmented exopod; exopod minute, armed with single apical seta. Labrum with wide and nearly straight cutting edge. Mandibula with narrow cutting edge and two-segmented palp; basis unarmed, endopod with four apical setae. Maxillular endopod absent. Maxilla with single endite on syncoxa; endopod minute, armed with two setae. Maxilliped three-segmented, unarmed. All swimming legs with three-segmented exopod. Endopod of first leg three-segmented, that of other legs one-segmented. First exopodal segment of all legs much longer than any other segments and without inner seta; second exopodal segment of first leg without inner seta, that of other legs with inner seta; third exopodal segment of all legs with two outer spines and no inner setae, except in fourth leg where one inner seta present. First endopodal segment of first leg larger than other two endopodal segments but smaller than first exopodal segment, armed with spiniform inner seta; endopodal segment of other legs very small, that of second and fourth legs armed with single apical spine, that of third leg with inner apical seta and outer apical spine. Basis of first leg in male with inner spine transformed, smooth and inflated distally; no other sexual dimorphism in swimming legs. Fifth leg similar in both sexes, with baseoendopod almost completely fused to somite and represented only by outer basal seta; exopod a minute but distinct segment, armed with single apical seta in female and (normally) with additional inner seta on male right leg. Sixth legs in male fused basally together and to somite, without armature or ornamentation.

Type and only species. *Inermipes humphreysi* Lee & Huys, 2002.

Remarks. This Western Australian genus is apparently very closely related to *Megastygonitocrella* **gen. nov.**, with its identical armature and segmentation of the swimming legs (the endopod of the second to fourth legs are one-segmented, with the respective armature formula 1.2.1) and has probably originated from an ancestor similar to some modern day *Megastygonitocrella* species. Also, the nature of these armature elements is exactly the same in the two genera. Lee & Huys (2002) justified the erection of the genus *Inermipes* Lee & Huys, 2002 mostly by the following four characters: an antennal exopod armed with only one apical element, basis of all swimming legs lacking the outer armature element, a highly reduced fifth leg and an unusually large spermatophore in the male. The first character was also observed in *Lucionitocrella yalleenensis* **gen. et sp. nov.** (see above), although the two species have very little in common, but also in some other ameirids that are completely unrelated (see Karanovic, 2006). Swimming legs without the outer armature element on the basis can be found in both *Psammonitocrella* Huys, 2009 species (see below), although only on the first and second legs. As can be witnessed in the descriptions of new species in this paper, the fifth leg can be variously reduced and sometimes much more so than in *Inermipes*, but it was previously also known to be completely reduced in *Stygonitocrella orghidani* (Petkovski, 1973) and *Reidnitocrella djirgalanica* (Borutzky, 1978) comb. nov. (see Petkovski 1973; Borutzky 1978). However, the enormous spermatophore, occupying nearly half of the body of *Inermipes humphreysi* Lee & Huys, 2002, is remarkable and it has not been reported so far in any other ameirid. Another autapomorphic feature of this genus is the enlarged first exopodal segment of all swimming legs. These two characters are sufficient to define *Inermipes* as a separate genus, but, being uninformative, were not included in the cladistic analysis of *Stygonitocrella s. l.* (see above).

The interestingly constricted habitus of *I. humphreysi* was also observed in one newly described species of the genus *Megastygonitocrella* **gen. nov.** (see below), but probably originated convergently in the two taxa. Reductions in the armature of the mouth appendages and antennula observed in *Inermipes* are also found in some other members of this group of freshwater ameirids and seem to be of limited phylogenetic importance, although many species have these characters only partly described or completely unknown. For example, a completely absent maxillular endopod was reported in *I. humphreysi*, *Kimberleynitocrella billhumphreysi* **gen. et sp. nov.**, *Psammonitocrella boultoni* Rouch, 1992 and *Stygonitocrella montana* (Noodt, 1965), but this appendage is unknown in 11 species (see Table 2, characters 10 & 11 and also Noodt (1965), Rouch (1992) and Lee & Huys (2002)). A first antennular segment without any armature is found in, besides *Inermipes*, both species of the genus *Psammonitocrella*, as well as in *Eduardonitocrella mexicana* (Suárez-Morales & Iliffe, 2005) comb. nov. It is one of the most important apomorphic characters (probably homoplastic!) that groups these dissimilar ameirids in the same clade (see the Discussion part of this paper), although they are probably not very closely related at all.

Two other problematic species on this branch are: *Neonitocrella insularis* (Miura, 1962) and *Stygonitocrella orghidani* (Petkovski, 1973). The latter one is so poorly described that we include it as *incertae sedis* in the newly redefined genus *Stygonitocrella* Reid, Hunt & Stanley, 2003 (see above). Both species share with *Inermipes* a reduced armature on the third endopodal segment of the first leg (Table 2, character 22), which probably is a homoplastic character as it was also found in *Stygonitocrella guadalfensis* Rouch, 1985 (see Miura 1962; Petkovski 1973; Rouch 1985).

Genus *Neonitocrella* Lee & Huys, 2002

Diagnosis emended. Medium sized Ameiridae, with cylindrical habitus and no distinct demarcation between prosome and urosome. Integument weakly chitinized and without cuticular windows; hyaline fringe of all somites smooth. First pedigerous somite incorporated into cephalothorax. Prosome only ornamented with sensilla, urosome additionally ornamented with short posterior ventral rows of small spinules. Genital somite free; genital field with single large copulatory pore, wide and short copulatory duct and two small semicircular seminal receptacles; single small genital aperture covered by fused reduced sixth legs. Anal operculum wide and convex, not reaching to posterior end of anal somite, ornamented with many minute spinules near posterior margin. Caudal rami conical, as long as greatest width and slightly divergent; dorsal seta inserted near posterior margin and very close to inner margin, about twice as long as ramus; proximal lateral seta arising somewhat dorsolaterally at middle; distal lateral seta arising close to posterior lateral margin; inner apical seta as long as ramus; principal apical setae with breaking plane. Antennula long and slender, eight-segmented in female and ten-segmented in male; with seta on first segment. Antenna composed of coxa, basis, two-segmented endopod and one-segmented exopod; exopod armed with two setae. Mandibula with narrow cutting edge and two-segmented palp; basis unarmed, endopod with five apical setae. Maxilla with single endite on syncoxa. Maxilliped three-segmented, prehensile. All swimming legs with three-segmented exopod. Endopod of first leg three-segmented; endopod of second and third swimming legs one-segmented, while that of fourth swimming leg reduced to a small knob. All exopodal segments of about same length; first exopodal segment of all legs, as well as second segment of first leg, without inner seta; second exopodal segment of second, third and fourth legs with inner seta; third exopodal segment of all legs with two outer spines and that of first, second and third legs without inner setae, but that of fourth leg with one inner seta. First endopodal segment of first leg large, almost reaching to posterior margin of second exopodal segment, armed with short spiniform inner seta; endopod of second and third legs slightly shorter than first exopodal segment, armed with inner apical plumose seta and much shorter outer apical spine. Basis of first leg in male probably with transformed inner spine; no other sexual dimorphism in swimming legs. Fifth leg similar in both sexes, with baseoendopod almost completely fused to somite and represented only by outer basal seta; exopod a minute but distinct segment, armed with two apical setae in female and with additional inner seta in male.

Type and only species. *Neonitocrella insularis* (Miura, 1962) [= *Nitocrella insularis* Miura, 1962].

Remarks. This genus was erected to accommodate a single Japanese species, *Nitocrella insularis* Miura, 1962, so far known only from the Ryukyu archipelago (Miura 1962). Lee & Huys (2002) pointed out its reduced endopod of the fourth leg, a bisetose antennal exopod and reduced fifth legs as the main distinguishing characters. As we have seen so far, the value of the last character is very limited and a very similar fifth leg was reported by Sterba (1973) for *Reidnitocrella pseudotianschanica* (Sterba, 1973) comb. nov. Similarly, a bisetose antennal exopod has been observed in a number of freshwater ameirids, including two unrelated species described in this paper. A completely absent endopod of the fourth swimming leg or its presence just as a small knob, is seen also in *Kimberleynitocrella billhumphreysi* **gen. et sp. nov.** (see above) and in both species of the genus *Psammonitocrella* Huys, 2009 (see Rouch 1992). This reduction apparently originated independently in these three lineages, as they have hardly anything else in common.

Miura (1962) listed a total of five males, but makes no comment on their variability or bilateral asymmetry. He illustrated only the right fifth leg and it is interesting to note its similarity with the condition in *Gordanitocrella* **gen. nov.** and *Inermipes* Lee & Huys, 2002, but in the description he only stated: "Exopodite of P5 different in shape from that of female and bears 3 setae". We would not be surprised if a closer examination of this and some additional material shows this character to be asymmetric. Lee & Huys (2002) in their diagnosis of the genus *Neonitocrella* Lee & Huys, 2002 mistakenly state that there is sexual dimorphism in "P3 endopod, ..., and in genital segmentation", but it is clear from the original drawings that the genital and first abdominal somites are separate in the female and Miura (1962) specifically states that in the male "endopodite of P3 not modified".

As we have explained in the Remarks section for the genus *Inermipes* Lee & Huys, 2002, *Neonitocrella* shares with *Psammonitocrella* a reduced armature of the third endopodal segment of the first leg, but this character is homoplastic and *Psammonitocrella* is a genus very well defined by a number of autapomorphic characters. *Neonitocrella* probably originated from some primitive *Megastygonitocrella*-like ancestor, as the armature of the endopodal segment of the second and third legs is the same as in *M. karamani* (Petkovski, 1959) comb. nov., although the latter species has a two-segmented endopod on these legs (one-segmented in *N. insularis*) and a one-segmented endopod of the fourth leg armed with a single apical spine. An endopod that is reduced to a small knob is technically still present, so we decided to use armature elements instead in the matrix presented above (Table 2). It is interesting to note that there is no normally developed apical endopodal segment without any armature elements in ameirids, which probably means that the reduction in the segment size and the loss of its last armature element occurred concurrently in a single event.

The genus *Neonitocrella* can be distinguished from all other ameirids by its unique armature formula of the ultimate endopodal segment of the second to fourth swimming legs, which is 2.2.0.

Genus *Eduardonitocrella* gen. nov.

Diagnosis. Medium sized Ameiridae, with robust and almost fusiform habitus but without distinct demarcation between prosome and urosome. Integument relatively strongly chitinized and without cuticular windows; hyaline fringe of all prosomites smooth, those of urosomites finely serrated. First pedigerous somite incorporated into cephalothorax. Prosome ornamented with sensilla and small pits only, urosome additionally ornamented with rows of small spinules. Genital somite free; genital field unknown. Anal operculum narrow and very short, reaching only to midlength of anal somite, ornamented with many small spinules near posterior margin. Caudal rami conical, as long as greatest width and slightly divergent; dorsal seta inserted close to inner margin, shorter than ramus; proximal lateral seta arising somewhat dorsolaterally at 2/3 and distal lateral seta arising posterolaterally, both very short; inner apical seta as long as ramus; principal apical setae with breaking plane. Antennula long and slender, eight-segmented in female (male unknown), without distal seta on first segment, but with proximal sensillum instead. Antenna composed of coxa, basis, two-segmented endopod and one-segmented exopod; exopod armed with two setae. Labrum with very narrow

cutting edge. Mandibula with narrow and pointed cutting edge and two-segmented small palp; basis unarmed, endopod with two apical setae. Maxillular endopod armed with single apical seta. Maxilla with single endite on syncoxa; endopod armed with single apical seta. Maxilliped three-segmented, unarmed. All swimming legs with three-segmented exopod. Endopod of first leg three-segmented; endopod of other legs one-segmented and about as long as first exopodal segment. All exopodal segments of about same length; first exopodal segment of all legs and second exopodal segment of first leg without inner seta; second exopodal segment of other legs with inner seta; third exopodal segment of first leg with three outer spines and no inner setae, that of other legs with two outer spines and without inner setae. First endopodal segment of first leg unarmed, long and slender, almost reaching to posterior margin of second exopodal segment; endopod of second leg with two slender apical setae, that of third and fourth legs with one inner and two apical setae. Fifth leg almost completely fused to somite, represented by two lateral knobs; inner knob, representing exopod, armed with two smooth slender setae; outer knob represents outer part of basis and armed with single seta; endopodal lobe absent.

Type and only species. *Eduardonitocrella mexicana* (Suárez-Morales & Iliffe, 2005) comb. nov. [= *Stygonitocrella (Eustygonitocrella) mexicana* Suárez-Morales & Iliffe, 2005].

Etymology. The genus is named in honour of Dr Eduardo Suárez-Morales (ECOSUR, Mexico), who described the type species. His first name is prefixed to the existing genus name *Nitocrella*. Gender feminine.

Remarks. A combination of plesiomorphic and apomorphic characters clearly define this genus. Its endopodal armature formula of second to fourth swimming legs (2.3.3) is unique in this group of freshwater ameirids, as is its very short anal operculum, which so far has been recorded only in marine and anchialine representatives of this family (the outgroup in our cladistic analysis being one of them; see above). Besides the outgroup, *Eduardonitocrella mexicana* (Suárez-Morales & Iliffe, 2005) comb. nov. is unique among the species examined in this study by the presence of an inner apical seta on the ultimate endopodal segment of the second leg (Table 2; character 27) and shares characters 37 and 46 only with *Lucionitocrella yalleenensis* **gen. et sp. nov**.

We have explained the different nature of the three armature elements on the third leg endopod in the Remarks section for the genus *Gordanitocrella* **gen. nov.**, as well as some major differences in the endopodal armature of the second and fourth legs between *Eduardonitocrella* and *Lucionitocrella* in the Remarks section for the latter genus. Most of these characters are plesiomorphic, as is the armature of the third exopodal segment of the first leg (character 19), which *Eduardonitocrella* shares only with *Gordanitocrella* and *Kimberleynitocrella* **gen. nov.** However, unlike these monospecific Australian genera, *Eduardonitocrella* has lost the inner seta on the first endopodal and second exopodal segments of the first leg (characters 17 & 20), as well as a number of reductions in the antennula, antenna and the mouth appendages. None of the latter reductions is unique. For example, a first antennular segment without armature (character 6) has been reported also in *Psammonitocrella* Huys, 2009 and *Inermipes* Lee & Huys, 2002, while a reduced armature on the mandibular endopod is recorded in *Psammonitocrella* and *Neonitocrella* Lee & Huys, 2002 (see Miura 1962; Rouch 1992; Lee & Huys 2002). Suárez-Morales & Iliffe (2005) erroneously reported a small proximal sensillum on the first antennular segment as a "short seta", but the real nature of this ornamentation (not armature) element is most probably a chemoreceptor. A very similar sensillum was observed on the male antennula of the below described *Megastygonitocrella ecowisei* **gen. et sp. nov.** which is probably homologous to the tubular pore in *Parapseudoleptomesochra tureei* Karanovic, 2006, the ordinary cuticular pore in *Abnitocrella eberhardi* Karanovic, 2006 or the "setule" in *Nitocrella trajani* Karanovic, 2004 (see Karanovic 2004a, 2006).

Eduardonitocrella differs also from other members of *Stygonitocrella s. l.* by its relatively robust habitus (with almost fusiform prosome), but the only autapomorphic features seem to be its extremely elongated and narrow labrum, as well as a very large mandibular coxa, which makes the mandibular palp look relatively very small. The fifth leg is also quite reduced in this genus, but we have discussed above the limited value of this character at the generic level.

Genus *Psammonitocrella* Huys, 2009

Diagnosis emended. Small and very slender Ameiridae, with cylindrical habitus and no distinct demarcation between prosome and urosome. Integument weakly chitinized and without cuticular windows; hyaline fringe of all somites smooth. First pedigerous somite incorporated into cephalothorax. Prosome ornamented only with sensilla, urosome additionally ornamented with rows of small spinules. Genital somite in female free; genital field with single large copulatory pore, wide copulatory duct and two small semicircular seminal receptacles; single small genital aperture covered by fused reduced sixth legs, without armature or ornamentation. Anal operculum unornamented, wide and convex, not reaching to posterior end of anal somite. Caudal rami slender, cylindrical and slightly divergent, longer than anal somite; dorsal seta inserted at 4/5 and close to inner margin, less than half ramus length; proximal lateral seta arising somewhat dorsolaterally at middle; distal lateral seta arising at 4/5 and laterally; inner apical seta minute; principal apical setae without breaking plane, outer one as long as or shorter than ramus. Antennula long and slender, eight-segmented in female and ten-segmented and geniculate in male; without seta on short first segment. Antenna composed of coxa, basis, two-segmented endopod and one-segmented exopod; exopod armed with three setae. Mandibula with narrow cutting edge and two-segmented palp; basis unarmed, endopod with three to five apical setae. Maxillular endopod armed with two apical setae or with reduced armature. Maxilla with single endite on syncoxa; endopod fused to basis, represented by surface seta. Maxilliped three-segmented, unarmed. All swimming legs with three-segmented exopod. Endopod of first leg three-segmented; endopod of second and third swimming legs two-segmented or one-segmented, while endopod of fourth swimming leg reduced to small knob or completely absent. All exopodal segments of about same length; first exopodal segment of all legs without inner seta, second with; second exopodal segment of first leg without outer spine; third exopodal segment of first leg with three outer spines and no inner setae, that of second leg with one or two outer spines and no inner setae, third leg with one outer spine and no inner setae and fourth leg with one outer spine and one or no inner setae. First endopodal segment of first leg unarmed, large, reaching to posterior margin of second exopodal segment; penultimate endopodal segment of second and third legs (if present) unarmed, ultimate segment with one apical seta; basis of first leg in male with unmodified inner spine; no other sexual dimorphism in swimming legs. Fifth legs similar in both sexes, fused to somite, with or without recognizable endopodal lobe and with recognizable exopodal lobe; endopodal lobe (if present) armed with one element, while exopodal lobe bears three, two or only one seta.

Type species. *Psammonitocrella boultoni* Rouch, 1992.

Other species. *Psammonitocrella longifurcata* Rouch, 1992.

Remarks. The genus was described by Rouch (1992) to accommodate two interstitial species collected in the hyporheic zone of an intermittent desert stream in Arizona, USA. As mentioned in the Introduction section, Rouch did not provide the mandatory type fixation, and the generic name *Psammonitocrella* was unavailable until Huys (2009) fixed *P. boultoni* Rouch, 1992 as the type species, thereby making the name available under his authorship. Huys (2009) also treated both species as new combinations and cited author names in parentheses, just as Reid *et al*. (2003) did for the genus *Stygonitocrella* Reid, Hunt & Stanley, 2003 (see the Remarks section for this genus). Although neither Article 11.9.3 nor Article 51.3 of the ICZN specifically addresses these two cases, the generic names are not different from the original ones, since the author attribution does not form part of a name in zoological nomenclature (Article 51.1). Therefore, we think parentheses should not have been used and it was at least an overstatement to refer to such cases as new combinations.

The familial placement of *Psammonitocrella* was questioned by Martínez Arbizu and Moura (1994), who removed it from the Ameiridae Monard, 1927 and regarded it as a sister-group of the family Parastenocarididae Chappuis, 1940. Lee & Huys (2002) proposed relocating it back to the Ameiridae, which has been accepted by subsequent workers (see Reid *et al.* 2003; Boxshall & Halsey 2004; Karanovic 2004a, 2006). The reason for all this confusion is the absence of sexual dimorphism on the inner basal spine of the first leg in this genus. The modification of this spine in male ameirids is one of the most important family

autapomorphies, but the condition observed in *Psammonitocrella* is probably paedomorphic and it was also recorded in the completely unrelated Australian genus *Archinitocrella* Karanovic, 2006. It apparently originated independently (as a convergence) in the two lineages and the main differences between them were explained by Karanovic (2006).

However, the genus *Psammonitocrella* remains well defined by many autapomorphic features, probably the most important one of them being the loss of the outer spine on the second exopodal segment of the first leg (Table 2, character 18). Unlike all other ameirids studied here, this genus also lacks the ancestral inner apical seta on the third exopodal segment of the second, third and fourth legs (characters 31 & 33), as well as the outer middle spine on the third exopodal segment of the third and fourth legs (character 32). A number of reductions were also reported for the mouth appendages, antennula and fifth legs, which makes it very difficult to establish a close relationship with other freshwater ameirids.

As we mentioned above, reduction of the endopod of the fourth swimming leg to a small knob has originated convergently in *Psammonitocrella, Kimberleynitocrella* **gen. nov.** and *Neonitocrella* Lee & Huys, 2002, while the first anennular segment without any armature is found in *Psammonitocrella, Eduardonitocrella* **gen. nov.** and *Inermipes* Lee & Huys, 2002 (see the Remarks sections for *Kimberleynitocrella* and *Eduardonitocrella*). Caudal rami longer than the anal somite are only found in one other species studied here (*Stygonitocrella sequoyahi* Reid, Hunt & Stanley, 2003), but this character seems to be of little phylogenetic importance outside the genus *Psammonitocrella*.

Several other important points one can learn from the two members of the genus *Psammonitocrella* are that characters of the fifth leg do not carry much phylogenetical importance (the variability of this character in *P. longifurcata* Rouch, 1992 is amazing) and the endopod of the second and third swimming legs can be reduced from a two-segmented state into a one-segmented state in a single event (at least in this group). However, the armature formula of the ultimate endopodal segment of the second to fourth legs is the same in both species (1.1.0) and is unique in *Stygonitocrella s. l.* That is why we decided to study the nature of the armature elements on the endopodal and exopodal segments, rather than using the segmentation of these rami as main generic characters, as was done in the past.

There are very few features to study in this group of highly reduced freshwater ameirids, where the number of homoplastic characters is expectedly very high. Different segmentation patterns between closely related species were also observed in the genera *Stygonitocrella* Reid, Hunt & Stanley, 2003 (as redefined above), *Reidnitocrella* **gen. nov.** and *Megastygonitocrella* **gen. nov.** One of the few plesiomorphic features of the genus *Psammonitocrella* is the inner seta on the second exopodal segment of the first leg (character 17), which shows that the ancestor of this genus could not have originated from a member of the genus *Megastygonitocrella*, but from some other, more primitive freshwater ameirid. The cladistic analysis presented in this paper shows that we should look for the ancestor of this North American genus somewhere in the genera *Reidnitocrella* or *Stygonitocrella*, the latter interestingly containing the only other North American representative of *Stygonitocrella s. l.*

Genus *Megastygonitocrella* gen. nov.

Diagnosis. Small to medium sized Ameiridae, with cylindrical habitus and no distinct demarcation between prosome and urosome. Integument with or without cuticular windows on cephalothorax and pedigerous somites; hyaline fringe of all prosomites smooth, those of urosomites smooth or finely serrated. First pedigerous somite incorporated into cephalothorax. Prosome ornamented only with large sensilla, urosome additionally ornamented with rows of small spinules. Genital somite free, partly or completely fused to first abdominal somite; genital field with single and relatively small copulatory pore, narrow copulatory duct and two small semicircular seminal receptacles; single small genital aperture covered by fused reduced sixth legs. Anal operculum convex, not reaching to posterior end of anal somite, smooth or ornamented with spinules near posterior margin. Caudal rami conical, as long as greatest width and slightly divergent; dorsal seta

inserted near posterior margin and very close to inner margin; proximal lateral seta arising somewhat dorsolaterally at middle; distal lateral seta arising posterolaterally; inner apical seta at least as long as ramus and smooth; principal apical setae pinnate, with breaking plane. Antennula long and slender or short and stout, eight-segmented in female (although last two segments sometimes partly or completely fused) and ten-segmented and geniculate in male; first segment with distal seta. Antenna composed of coxa, basis, two-segmented endopod and one-segmented exopod; exopod armed with one to three setae. Labrum with relatively narrow and convex cutting edge. Mandibula with narrow cutting edge and two-segmented palp; basis unarmed or armed with one seta, endopod with four to five apical setae. Maxillular endopod armed with single apical seta. Maxilla with single endite on syncoxa; endopod minute, armed with two apical setae. Maxilliped three-segmented, armed with at least one seta on syncoxa and one on endopod. All swimming legs with three-segmented exopod. Endopod of first leg three-segmented; endopod of second and third swimming legs two-segmented or one-segmented, while endopod of fourth swimming leg always one-segmented. All exopodal segments of about same length; first exopodal segment of all legs without inner seta; second exopodal segment of first leg without inner seta, that of other legs with inner seta; third exopodal segment of all legs with two outer spines, that of first, second and third legs without inner setae, that of fourth leg with one, two or no inner setae. First endopodal segment of first leg large, reaching to at least midlength of third exopodal segment, armed with short spiniform inner seta; penultimate endopodal segment of second and third legs (if present) always unarmed; ultimate segment of second leg armed with outer apical spine and inner apical seta or just with apical spine, that of third leg always with outer apical spine and inner apical seta and that of fourth leg always with single apical spine. Basis of first leg in male with inner spine transformed, smooth and inflated distally; only other form of sexual dimorphism in swimming legs involves somewhat shorter inner apical seta on ultimate endopodal segment of third leg in male. Fifth leg with maximum of four setae on exopod in female (and additional inner seta in male) and three elements on endopodal lobe; most species typically with armature variously reduced, to minimum of three setae on exopod and no elements on endopodal lobe, and displaying various fusion patterns (with maximum being completely fused to somite, represented by two small knobs). Sixth legs in male fused together medially and to somite, each armed with one or two setae.

Type species. *Megastygonitocrella trispinosa* (Karanovic, 2006) comb. nov. [= *Stygonitocrella trispinosa* Karanovic, 2006].

Other species. *Megastygonitocrella unispinosa* (Karanovic, 2006) comb. nov. [= *Stygonitocrella unispinosa* Karanovic, 2006]; *Megastygonitocrella bispinosa* (Karanovic, 2006) comb. nov. [= *Stygonitocrella bispinosa* Karanovic, 2006]; *Megastygonitocrella ljovuschkini* (Borutzky, 1967) comb. nov. [= *Nitocrella ljovuschkini* Borutzky, 1967]; *Megastygonitocrella petkovskii* (Pesce, 1985) comb. nov. [= *Stygonitocrella petkovskii* Pesce, 1985]; *Megastygonitocrella karamani* (Petkovski, 1959) comb. nov. [= *Nitocrella karamani* Petkovski, 1959]; *Megastygonitocrella colchica* (Borutzky & Michailova-Neikova, 1970) comb. nov. [= *Nitocrella colchica* Borutzky & Mihailova-Neikova, 1970]; *Megastygonitocrella dec* **sp. nov.**; *Megastygonitocrella ecowisei* **sp. nov.**; *Megastygonitocrella pagusregalis* **sp. nov.**; *Megastygonitocrella kryptos* **sp. nov.**

Etymology. The genus name comes from the Greek adjective "megas" (meaning "large" and referring to the largest number of species in the group of genera studied here), prefixed to the existing genus name *Stygonitocrella*. Gender feminine.

Remarks. The genus *Megastygonitocrella* **gen. nov.** represents a closely related group of species of *Stygonitocrella s. l.*, of which all, except one member, possess the same armature formula of the ultimate endopodal segment of the second to fourth legs (1.2.1). However, it is not just the number of armature elements that unites these species, but also their nature. All of these species have the ancestral outer subapical spine as their only element on the endopod of the second and fourth legs (Table 2, characters 25 & 43), while the endopod of the third leg also has the ancestral outer apical seta (characters 35 & 36). The genera *Stygonitocrella* Reid, Hunt & Stanley, 2003 (as revised above) and *Psammonitocrella* Huys, 2009 also have

only one apical element on the endopod of the second leg, but it represents the ancestral outer apical seta (character 26) rather than the outer subapical spine.

Most species of the genus *Megastygonitocrella* also have a one-segmented endopod on the second to fourth legs, except for *M. colchica* (Borutzky & Michailova-Neikova, 1970) comb. nov., *M. petkovskii* (Pesce, 1985) comb. nov. and *M. karamani* (Petkovski, 1959) comb. nov. which have the endopod of the second and third legs two-segmented. The latter is also the only species with the armature formula 2.2.1 instead of 1.2.1. These two plesiomorphic characters were not enough to exclude *M. karamani* from the genus in our cladistic analysis and we think this species exhibits what the ancestor of this group looked like, at least in the characters associated with the swimming legs. That is why we think *Neonitocrella* Lee & Huys, 2002 is the closest living relative of *Megastygonitocrella* (see the Remarks section for *Neonitocrella*). Unfortunately, *Neonitocrella insularis* (Miura, 1962), *M. colchica, M. petkovskii* and *M. karamani* are incompletely described (see Petkovski 1959; Miura 1962; Borutzky & Michailova-Neikova 1970; Pesce 1985) and many of their characters could not be compared or included in the cladistic analysis. Note that Pesce (1985) erroneously described the third leg of *M. petkovskii* as the second one and *vice versa*, which we attribute to a simple error during the dissection process. It seems that the segmentation of the endopod of the second and third swimming legs (effectively the loss of the penultimate segment) can be reduced in a single event (see also the Remarks section for the genus *Psammonitocrella*), as *M. colchica* apparently is very closely related to *M. ljovuschkini* (Bortuzky, 1967) comb. nov. and the two species also live not far away from each other.

Members of the genus *Megastygonitocrella* are found in Australia (Pilbara region in Western Australia and Pioneer Valley in Queensland), Southern Europe (Slovenia and the island of Lesbos, Greece) and the Caucasus (Western Gruzia and the Russian Krasnodarsk Region), which would suggest a Tethyan origin of this group. This zoogeographical connection is well recognized for many Australian stygofaunal elements (Karanovic 2006; Humphreys 2008). All species of *Megastygonitocrella* have lost the inner seta on the second exopodal segment of the first leg, and have only two outer spines on all swimming legs and no inner armature elements on the third exopodal segment of the first, second and third legs.

Key to species of *Megastygonitocrella* gen. nov.

1	Endopod of second leg with single apical element	2
-	Endopod of second leg with two apical elements	*M. karamani* (Petkovski, 1959)
2	Endopod of second and third legs two-segmented	3
-	Endopod of second and third legs one-segmented	4
3	Inner seta on second endopodal segment of second leg absent	*M. petkovskii* (Pesce, 1985)
-	This seta present	*M. colchica* (Borutzky & Michailova-Neikova, 1970)
4	Fifth leg with unarmed endopodal lobe	5
-	Fifth leg endopodal lobe armed	7
5	Fifth leg exopod free	6
-	Fifth leg exopod fused to somite	*M. pagusregalis* **sp. nov.**
6	Habitus constricted at genital somite	*M. dec* **sp. nov.**
-	Habitus not constricted	*M. kryptos* **sp. nov.**
7	Third exopodal segment of fourth leg with one or two inner setae	8
-	Third exopodal segment of fourth leg without inner setae	*M. ljovuschkini* (Borutzky, 1967)
8	Third exopodal segment of fourth leg with one inner seta	9
-	Third exopodal segment of fourth leg with two inner setae	*M. bispinosa* (Karanovic, 2006)
9	Integument without cuticular windows	10
-	Cuticular windows present	*M. trispinosa* (Karanovic, 2006)
10	Fifth leg endopodal lobe with two armature elements	*M. ecowisei* **sp. nov.**
-	Fifth leg endopodal lobe with only one element	*M. unispinosa* (Karanovic, 2006)

***Megastygonitocrella dec* sp. nov.**
(Figs 10–11)

Type material. Holotype, adult female dissected on one slide (WAM C37348); allotype, adult male dissected on one slide (WAM C37349); paratypes: one female dissected on one slide (WAM C37350) and one male, two females and 11 copepodids preserved in 70% ethanol (WAM C37351); Australia, Western Australia, Pilbara region, Yule River, bore GNHSLK1448B, 18 November 2003, leg. J. Cocking & M. Scanlon, 21°36’14”S 118°49’01”E.

Description. FEMALE (HOLOTYPE). Body length, excluding appendages and caudal setae, 0.497 mm. Preserved specimen colourless. Nauplius eye absent. Prosome (Fig. 10A) comprising cephalothorax and three free pedigerous somites, while urosome comprising fifth pedigerous somite, completely distinct genital somite and four abdominal somites. First two urosomites (Fig. 10B) narrower than previous and subsequent somites, which makes for unusually constricted habitus in dorsal view and distinct demarcation between prosome and urosome; prosome/urosome ratio 0.9 and greatest width at second pedigerous (first free) prosomite. Body length/width ratio about 5.1. Free pedigerous somites without pronounced lateral or dorsal expansions. Integument weakly chitinized and without cuticular windows. Rostrum (Fig. 10A) extremely small, membranous, not demarcated at base and ornamented with two dorsal sensilla on anterior margin.

Cephalothorax (Fig. 10A) with completely incorporated first pedigerous somite, quadriform in dorsal view, about as long as wide; represents 19% of total body length. Surface of cephalic shield and tergites of three free pedigerous somites ornamented only with several large sensilla. Hyaline fringe of all prosomites narrow and smooth. Fifth pedigerous (first urosomal) somite ornamented with two large dorsal sensilla and two smaller lateral sensilla on each side; hyaline fringe smooth both dorsally and laterally (Fig. 10A). Large sclerotized joint (Figs 10A–B) present between fifth pedigerous and genital somites and visible both ventrally and dorsally.

Genital somite (Fig. 10B) approximately three times as wide as long (ventral view); ornamented only with four posterior dorsal sensilla. Hyaline fringe smooth and very narrow both ventrally and dorsally. Genital field with single small copulatory pore at about midlength, extremely short copulatory duct and two ovoid seminal receptacles, posterior part of which reaches well beyond copulatory pore, to about 2/3 of somite length. Relatively large genital aperture covered by fused reduced sixth legs, represents 46% of somite width. Third urosomite (Figs 10A–B) ornamented with 10 large posterior sensilla (two dorsal, four lateral (two on each side) and four ventral), two large anterior lateral sensilla (one on each side) and two lateral cuticular pores (also one on each side) at midlength; posterior margin of this somite represents widest part of urosome in ventral view; hyaline fringe smooth. Fourth urosomite with 10 large posterior sensilla (two dorsal, four lateral and four ventral), two lateral pores (one on each side) and two slightly arched, short ventrolateral rows of spinules at midlength. Preanal somite about as long as previous one, but narrower, 1.8 times as wide as long, ornamented only with two short rows of spinules similar to previous somite, but shorter and closer to each other. Anal somite (Figs 10A–B) ornamented with pair of large dorsal sensilla, two short ventral rows of spinules in anterior half and posterior row of spinules interrupted between caudal rami. Anal operculum unornamented, convex, not reaching to posterior end of anal somite, represents 50% of somite's width. Anal sinus smooth and widely opened.

Caudal rami (Figs 10A–B) short and conical, slightly shorter than their greatest width (ventral view), somewhat divergent, with space between them about one ramus width, with small diagonal chitinous ridge dorsally, armed with seven setae (three lateral, three apical and one dorsal). Ornamentation consists of two spinules each at base of dorsal and distal lateral seta, one ventral cuticular pore and posterior ventral row of seven or eight small spinules. Dorsal seta inserted almost at posterior end and close to inner margin, slender, smooth, 1.5 times as long as caudal ramus, triarticulate at its base. Proximal lateral seta arising somewhat dorsolaterally at 2/5 of ramus length, 0.8 times as long as dorsal one and 1.2 times as long as distal lateral seta, which arises at 4/5 of ramus length. Inner apical seta very slender and smooth, slightly shorter than ramus. Both principal setae sparsely pinnate at distal end, with breaking plane.

FIGURE 10. *Megastygonitocrella dec* **gen. et sp. nov.**, holotype female: A—habitus, lateral view; B—urosome, ventral view; C—antennula; D—antenna; E—labrum; F—mandibula; G—maxilla; H—maxilliped. Scales = 0.1 mm.

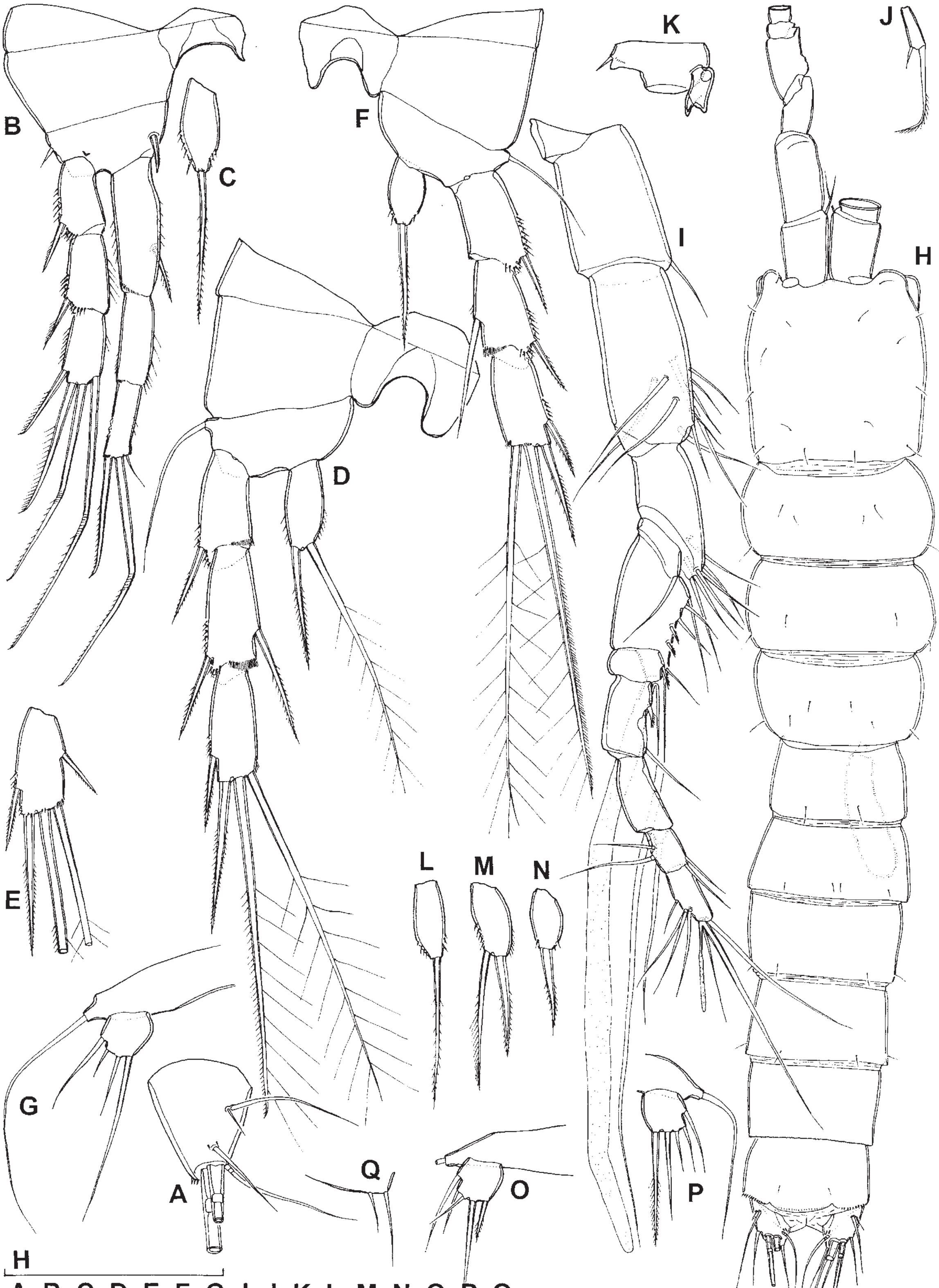

FIGURE 11. *Megastygonitocrella dec* **gen. et sp. nov.**, A–G, holotype female; H–Q, allotype male: A—left caudal ramus, lateral view; B—first swimming leg; C—endopod of second swimming leg; D—third swimming leg; E—third exopodal segment of right fourth leg; F—left fourth swimming leg; G—right fifth leg; H—habitus, dorsal view; I—antennula; J—exopod of antenna; K—basis of first swimming leg; L—endopod of second swimming leg; M—endopod of third swimming leg; N—endopod of fourth swimming leg; O—right fifth leg; P—left fifth leg; Q—left sixth leg. Scales = 0.1 mm.

Antennula (Fig. 10C) eight-segmented, unornamented, slender, approximately twice as long as cephalothorax. Very long slender aesthetasc on fourth segment reaches beyond tip of appendage for more than length of last five segments combined and fused basally with large subapical seta; much smaller and even more slender apical aesthetasc on eighth segment fused basally to two apical setae. Setal formula: 1.8.6.3.2.2.4.7. All setae smooth and without breaking plane; only three setae on eighth segment biarticulating on basal part. Length ratio of antennular segments, from proximal to distal end and along caudal margin, 1 : 1.2 : 1 : 0.9 : 0.6 : 0.7 : 0.4 : 0.5.

Antenna (Fig. 10D) composed of coxa, basis, two-segmented endopod and one-segmented exopod. Coxa very short, unornamented. Basis about 1.4 times as long as wide, unornamented and unarmed. First endopodal segment 1.4 times as long as basis, 1.8 times as long as wide, unornamented and unarmed. Second endopodal segment longest, 1.4 times as long as first and 3.3 times as long as wide, armed laterally with two bipinnate spines flanking thin seta; apical armature consisting of five geniculate setae, longest one fused basally to additional smaller, slender and smooth seta; ornamentation consists of few spinules along anterior distal surface and two fringes on posterior surface. Exopod one-segmented, 0.6 times as long as basis and 2.3 times as long as wide, unornamented but armed with two setae; inner apical seta bipinnate, slender and 4.6 times as long as outer curved and smooth seta.

Labrum (Fig. 10E) not very large when compared to cephalothorax, trapezoidal, rigidly sclerotized, with relatively narrow and convex cutting edge, ornamented with one apical row of small spinules in between two subapical rows of strong spinules. Two ellipsoid fields of gustatory papillae visible on dorsal (posterior) surface.

Paragnaths not mounted properly to allow detailed observation.

Mandibula (Fig. 10F) very small, with wide cutting edge on elongated coxa, armed with numerous small teeth in between three ventral coarse teeth and one dorsal unipinnate seta. Palp uniramous, comprising basis and one-segmented endopod. Basis very elongated, unarmed and unornamented, 2.8 times as long as wide and 2.5 times as long as endopod. Endopod small and unornamented, about 1.9 times as long as wide; armed apically with five slender smooth setae.

Maxillula very similar to that of *Gordanitocrella trajani* **gen. et sp.nov.** (Fig. 5I).

Maxilla (Fig. 10G) small, unornamented, with proximal endite on syncoxa absent; distal endite well developed, highly mobile, armed with one pinnate spine and two smooth subequal setae. Basis drawn out into long claw, with shorter spiniform seta at its base. Endopod represented by minute segment, armed with two smooth, subequal apical setae.

Maxilliped (Fig. 10H) with short syncoxa ornamented with few large spinules and armed with single smooth seta near inner distal corner, 1.4 times as long as wide. Basis 2.4 times as long as wide and 1.7 times as long as syncoxa, unarmed. Endopod represented by long curved claw, ornamented distally with row of spinules along concave side; with thin seta at base.

All swimming legs with three-segmented exopod; endopod of first leg three-segmented (Fig. 11B), endopod of other swimming legs one-segmented (Figs 11C–F). Armature formula of swimming legs as follows (inner/outer element; inner/terminal/outer element):

	Exopod			Endopod		
Segments	1	2	3	1	2	3
First leg	0/1	0/1	0/2/2	1/0	0/0	1/1/1
Second leg	0/1	1/1	0/2/2	0/1/0	-	-
Third leg	0/1	1/1	0/2/2	1/1/0	-	-
Fourth leg	0/1	1/1	0(1)/2/2	0/1/0	-	-

Intercoxal sclerite of all swimming legs small, with concave distal margin and without surface ornamentation. Praecoxae and coxae of all legs unarmed and unornamented. Basis of each leg unornamented; armed with small outer spine on first and second swimming legs and smooth outer seta on third and fourth legs; first leg with stout spine on inner margin at about 3/5 of segment length. All exopodal and endopodal

segments ornamented with spinules along outer margin and on outer distal corner; endopod and some exopodal segments with spinules along inner margin as well; inner distal corner of first and second exopodal segments of most legs with frilled membrane. All exopodal segments of about same length. First endopodal segment of first swimming leg (Fig. 11B) about three times as long as wide and reaching to 2/3 of second exopodal segment; endopod significantly longer than exopod. Endopod of second and third swimming legs about as long as first exopodal segment; that of fourth leg somewhat shorter. Apical armature element(s) on first leg geniculate, pinnate on outer (concave) side and smooth on inner side. Third exopodal segment of other legs with plumose inner apical seta and heterogeneously ornamented outer apical seta (plumose on inner margin, pinnate on outer; transitional stage between seta and spine). Apical endopodal element of second, third and fourth leg spiniform, but longer than segment; inner seta on endopod of third leg slender, plumose and about twice as long as apical element. Inner element on second exopodal segment short and spiniform, while all outer exopodal spines strong and bipinnate.

Fifth legs (Figs 10B, 11G) biramous but baseoendopods fused together medially, although distinct from somite. Endopodal lobe not recognizable, forming straight smooth hyaline fringe and without armature or ornamentation. Basal outer seta slender and smooth, on long setophore. Exopod a distinct segment, ovoid, small, about as long as its maximum width, unornamented but armed with four smooth setae; length ratio of exopodal setae from inner to outer side 1 : 0.36 : 0.18 : 0.5. Longest exopodal seta strongest, 0.7 times as long as outer basal seta.

Sixth legs (Fig. 10B) completely fused together, forming simple operculum covering single gonopore, each armed with minute smooth seta.

MALE (ALLOTYPE). Body length, excluding caudal setae, 0.442 mm. Habitus (Fig. 11H), ornamentation of prosomites, rostrum, colour and nauplius eye similar to female. Hyaline fringe of all somites smooth. Body constricted at middle as in female, with fifth pedigerous somite narrower than fourth pedigerous or genital somites.

Genital somite twice as wide as long. Single large spermatophore (Fig. 11H) longitudinally placed inside fifth pedigerous and genital somites. Third and fourth urosomites with spinules and sensilla pattern same as in female; preanal somite without dorsal surface ornamentation as in female. Anal operculum (Fig. 11H) with posterior row of many minute spinules.

Caudal rami (Fig. 11H) slightly shorter and not divergent, but armature and ornamentation very similar to female.

Antennula (Fig. 11I) unornamented, long and slender, ten-segmented, not strongly geniculate, with geniculation between seventh and eighth segments. Long aesthetasc on apical acrothek of fifth segment homologous to aesthetasc on fourth segment in female. Smaller aesthetasc on tenth segment fused basally to two apical setae. Armature of first, ninth and tenth segments similar to female. Setal formula: 1.10.6.1.7.1.2.1.4.7. Majority of setae smooth and slender; two setae on fifth segment, one on sixth and one on seventh very short, spiniform and unipinnate. Outer (caudal) setae on ninth and tenth segments biarticulating on basal part; no setae with breaking plane.

Antenna (Fig. 11J), labrum, mandibula, maxillula, maxilla, maxilliped, second swimming leg (Fig. 11L) and fourth swimming leg (Fig. 11N) similar to female.

Basis of first swimming leg (Fig. 11K) with inner spine modified, smooth, inflated and apically transformed into a complex tridimensional structure, similar to twisted but widely open pincers.

Endopod of third swimming leg (Fig. 11M) with inner seta unipinnate and significantly shorter than in female.

Fifth legs (Figs 11O–P) similar to female, except exopod additionally armed with innermost bipinnate seta; second innermost seta (homologous to innermost seta on female exopod) also proportionally shorter. Outer basal seta shorter than in female.

Sixth legs (Fig. 11Q) narrowly fused basally together and indistinct from somite, each armed with two slender smooth setae; outer seta 1.8 times as long as inner one.

Variability. Body length of females ranges from 0.487 mm to 0.497 mm (0.492 mm average; n = 4), while

only two males were collected and studied (0. 442 and 0.445 mm long). Both males exhibit asymmetry in the length of the innermost spiniform seta on the fifth leg exopod (Figs 11O–P). All males and females have the third exopodal segment of the fourth swimming leg with an inner seta present on one leg but absent on the opposite one (Figs 11D–E). It is interesting that all females have a smooth anal operculum, while both examined males have a posterior row of minute spinules.

Etymology. The specific name is dedicated to the Western Australian Government Department of Environment and Conservation (DEC), who collected the material and partly funded the preparation of this paper. It comprises an arbitrary combination of letters that can be treated as a Latin word and that should be conceived as a noun of feminine gender.

Remarks. The one-segmented endopod of the second to fourth swimming legs, armed only with the ancestral outer subapical spine on the second and fourth legs and additionally with an outer apical seta on the third (formula 1.2.1), leave no doubt that this species belongs to the genus *Megastygonitocrella* **gen. nov.** In fact, *M. dec* **sp. nov.** has the same segmentation and almost the same armature formula (the only difference being the number of inner elements on the third exopodal segment of the fourth leg) as the Caucasian *M. ljovuschkini* (Borutzky, 1967) comb. nov. and six other Australian representatives: *M. ecowisei* **sp. nov.**, *M. pagusregalis* **sp. nov.**, *M. kryptos* **sp. nov.**, *M. trispinosa* (Karanovic, 2006) comb. nov., *M. bispinosa* (Karanovic, 2006) comb. nov. and *M. unispinosa* (Karanovic, 2006) comb. nov. However, it is easily distinguished from all these congeners by a constricted habitus, reduced armature of the antennal exopod, very long mandibular basis, completely free genital somite in the female and the unusually robust inner basal spine on the first swimming leg in the male. *Megastygonitocrella dec* can be easily distinguished further from *M. ecowisei, M. trispinosa, M. bispinosa* and *M. unispinosa* by its unarmed fifth leg endopodal lobe. It differs additionally from *M. pagusregalis* by having the fifth leg free (completely fused to somite in the latter species), a much more elongated antennula (very short in *M. pagusregalis*) and different ornamentation of the urosomites. Finally, *M. dec* can be additionally distinguished from *M. kryptos* by the shape of its caudal rami, ornamentation of the anal operculum and the number of armature elements on the fifth leg exopod.

***Megastygonitocrella ecowisei* sp. nov.**
(Figs 12–14)

Type material. Holotype, adult female dissected on one slide (WAM C37352); allotype, adult male dissected on one slide (WAM C37353); paratypes: one female dissected on one slide together with *Megastygonitocrella trispinosa* (Karanovic, 2006) (WAM C37354) and two copepodids preserved in 70% ethanol (WAM C37355); Australia, Western Australia, Pilbara region, Atlas Iron Mine, bore PDPIEZ11B, sample #4110, 10 December 2007, leg. C. Foord & G. Benisson, 20°14'25"S 119°08'40"E.

Description. FEMALE (HOLOTYPE). Body length, excluding appendages and caudal setae, 0.527 mm. Preserved specimen colourless. Nauplius eye absent. Prosome (Fig. 13I) comprising cephalothorax and three free pedigerous somites, while urosome comprising fifth pedigerous somite, genital double-somite and three abdominal somites (Fig. 12A). Habitus cylindrical, slender, without distinct demarcation between prosome and urosome; greatest width at first free pedigerous somite. Body length/width ratio about 4.9; cephalothorax only slightly wider than genital double-somite. Free pedigerous somites without pronounced lateral or dorsal expansions. Integument not strongly chitinized and without cuticular windows. Rostrum very small and membranous, linguiform, about as long as wide, ornamented with two dorsal sensilla near anterior margin.

Cephalothorax (Fig. 13I) with completely incorporated first pedigerous somite, quadriform in dorsal view, slightly longer than wide. Surface of cephalic shield and tergites of three free pedigerous somites ornamented only with several large sensilla. Hyaline fringe of all prosomites narrow and smooth. Fifth pedigerous (first urosomal) somite ornamented with two large dorsal sensilla and two smaller lateral sensilla on each side; hyaline fringe smooth both dorsally and laterally. Large sclerotized joint (Fig. 12A) present between fifth pedigerous and genital double somites and visible both ventrally and dorsally.

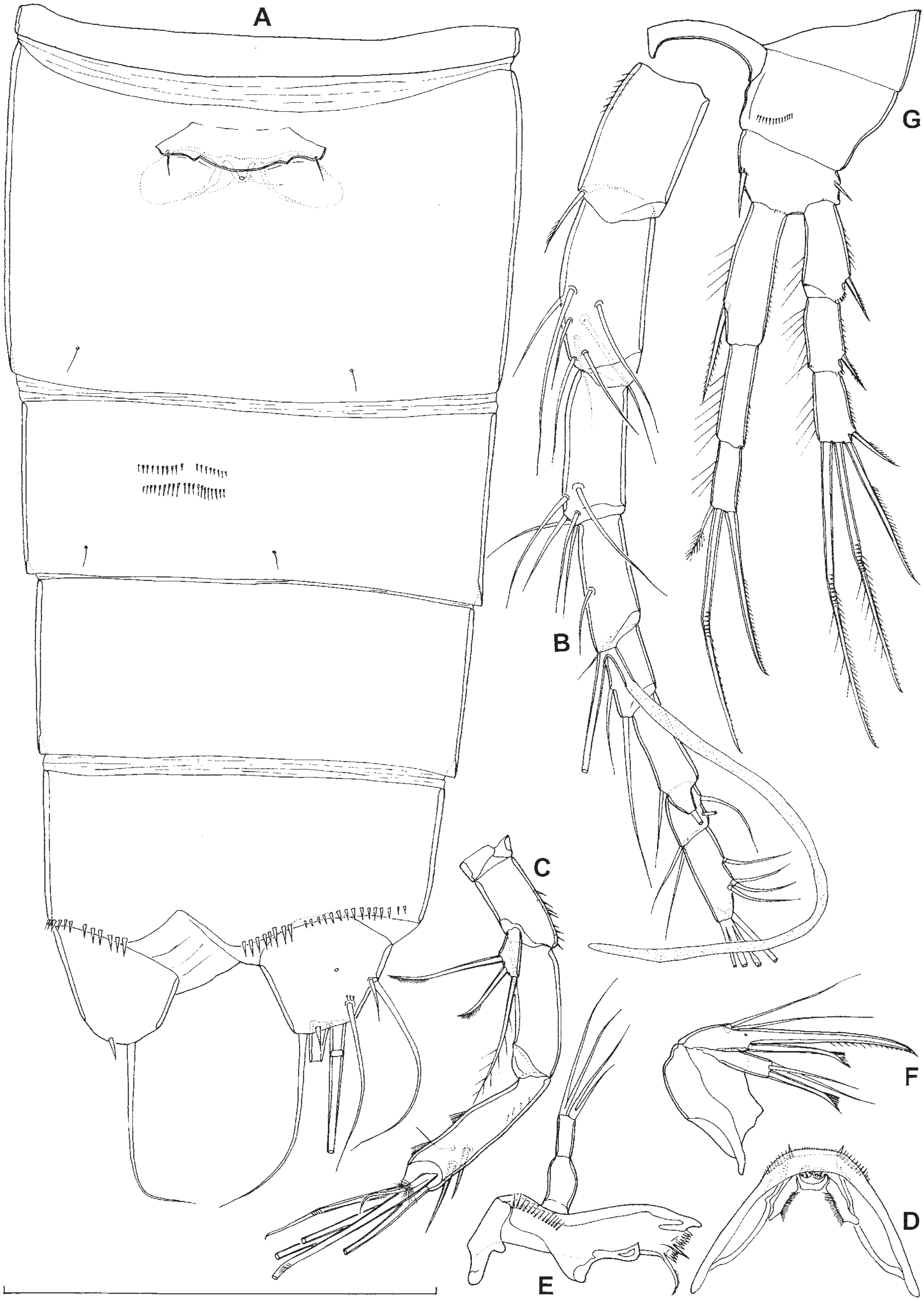

FIGURE 12. *Megastygonitocrella ecowisei* **gen. et sp. nov.**, holotype female: A—compressed abdomen, ventral view; B—antennula; C—antenna; D—labrum; E—mandibula; F—maxilla; G—first swimming leg. Scale = 0.1 mm.

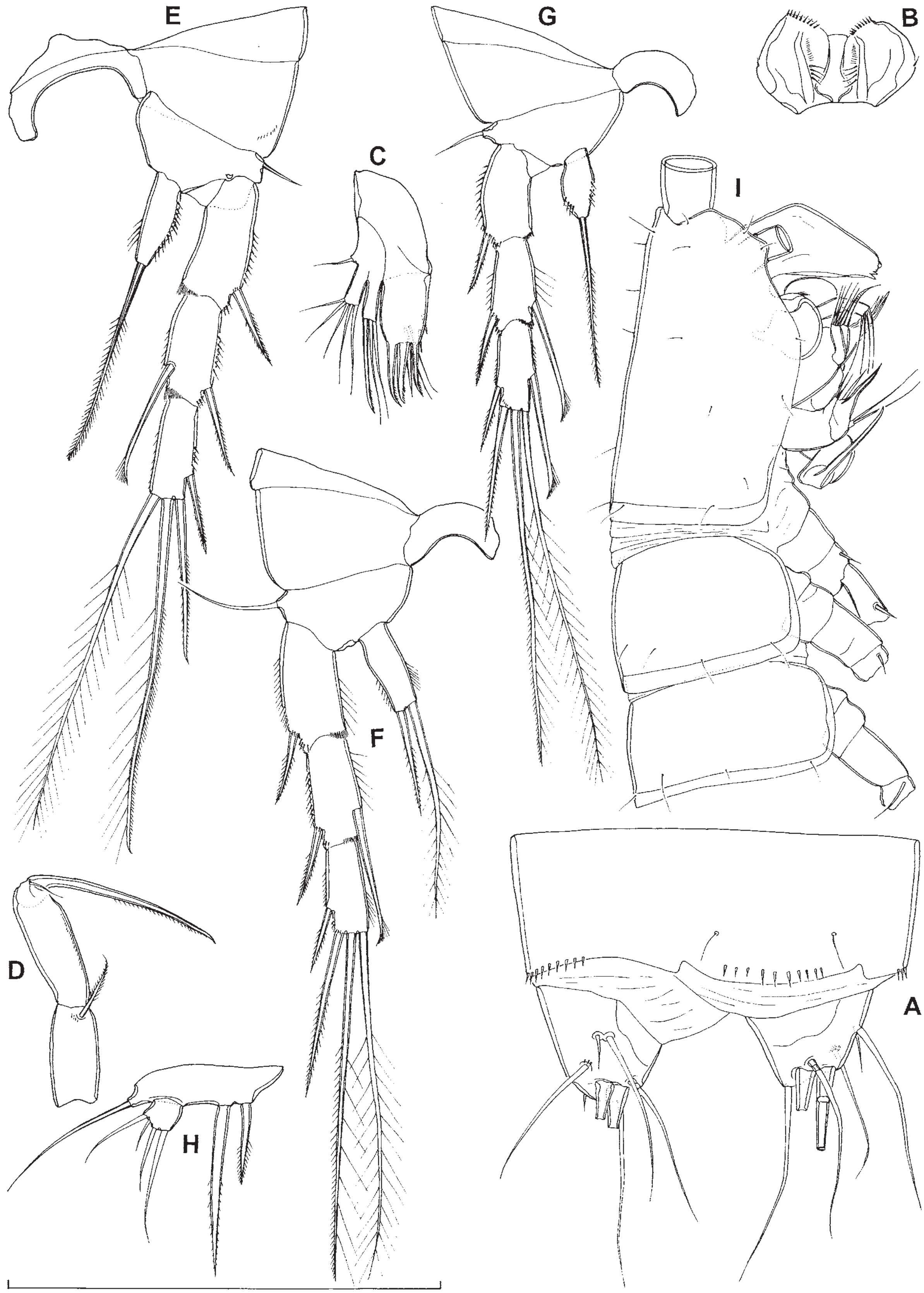

FIGURE 13. *Megastygonitocrella ecowisei* **gen. et sp. nov.**, A–H, holotype female; I, allotype male: A—anal somite and caudal rami, dorsal view and somewhat compressed; B—paragnaths; C—maxillula; D—maxilliped; E—second swimming leg; F—third swimming leg; G—fourth swimming leg; H—fifth leg; I—cephalothorax and two free prosomites, lateral view. Scale = 0.1 mm.

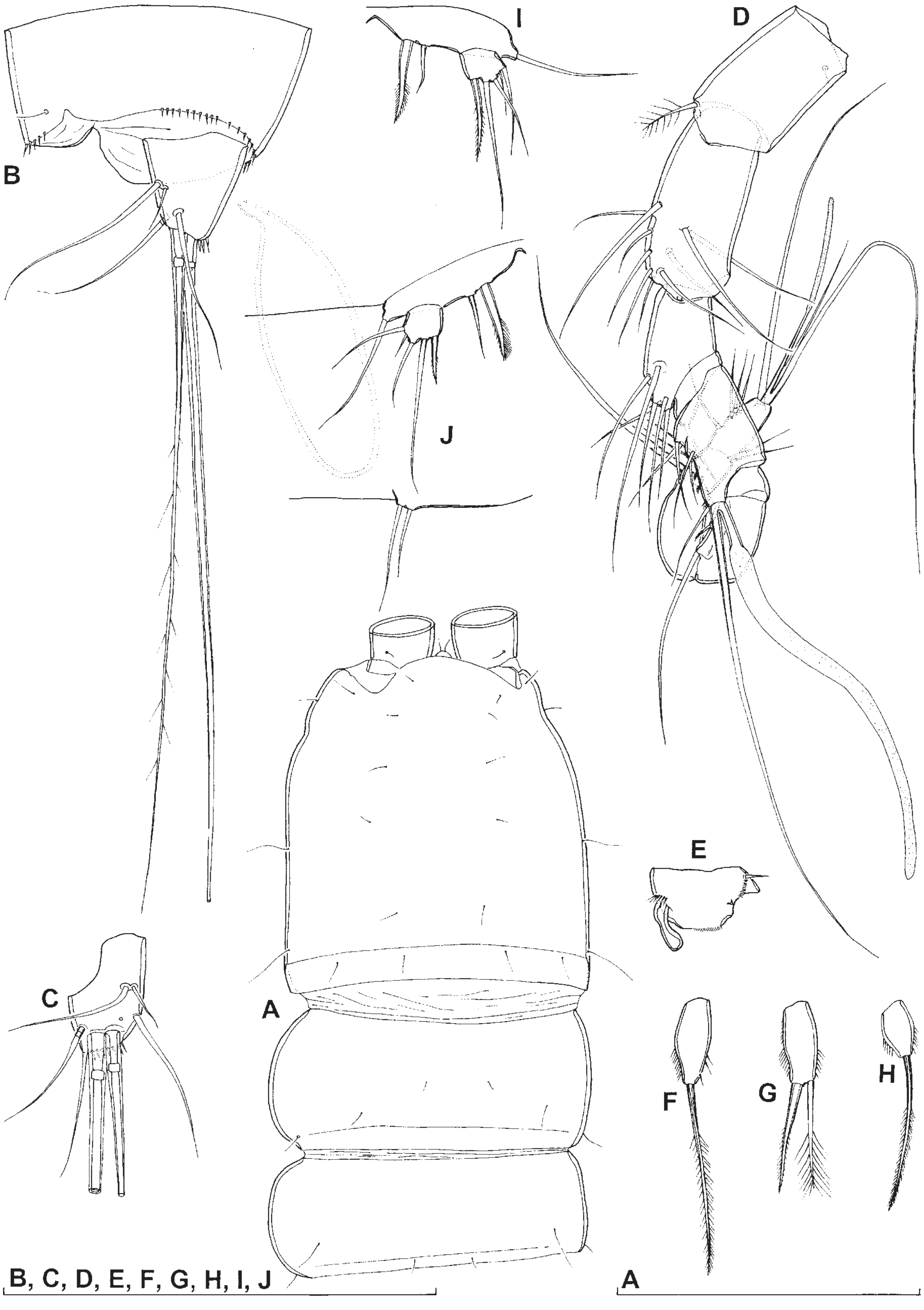

FIGURE 14. *Megastygonitocrella ecowisei* **gen. et sp. nov.**, allotype male: A—cephalothorax and two free prosomites, dorsal view; B—anal somite and right caudal ramus, lateral view; C—right caudal ramus, dorsal view; D—antennula; E—basis of first swimming leg; F—endopod of second swimming leg; G—endopod of third swimming leg; H—endopod of fourth swimming leg; I—left fifth leg; J—right fifth and sixth legs, with spermatophore inside. Scales = 0.1 mm.

Genital double-somite (Fig. 12A) somewhat wider than long (ventral view), without visible suture or constriction showing original segmentation; ornamented just with six large dorsal sensilla (two at middle, four near posterior margin) and two posterior ventral sensilla. Hyaline fringe completely smooth both ventrally and dorsally. Genital field with single minute copulatory pore at about first quarter of double-somite length, strongly sclerotized but very short copulatory duct and two ovoid seminal receptacles. Single small genital aperture covered by fused reduced sixth legs, represents 38% of somite width; copulatory pore situated very close to gonopore. Third urosomite ornamented with four large sensilla near posterior margin (two dorsal and two ventral) and two parallel ventral rows of minute spinules at midlength; hyaline fringe smooth. Preanal somite without surface ornamentation and with smooth hyaline fringe dorsally and ventrally. Anal somite (Figs 12A, 13A) ornamented with pair of large dorsal sensilla and posterior row of small spinules interrupted ventrally between caudal rami. Anal operculum (Fig. 13A) convex, not reaching to posterior end of anal somite, represents 47% of somite's width; ornamented near its posterior margin with 10 small spinules of about same size as spinules on posterior dorsal margin of anal somite. Anal sinus smooth and widely opened.

Caudal rami (Figs 12A, 13A) short and conical, slightly shorter than their greatest width (ventral view), somewhat divergent, with space between them about one ramus width, with small diagonal chitinous ridge dorsally; armed with seven setae (three lateral, three apical and one dorsal). Ornamentation consists of three minute spinules at base of distal lateral seta and single larger spinule on posterior ventral margin. Dorsal seta inserted almost at posterior end and close to inner margin, slender, smooth, 1.8 times as long as caudal ramus, triarticulate at its base. Proximal lateral seta arising somewhat dorsolaterally at midlength, about as long as dorsal one and only slightly longer than distal lateral seta, which arises at 3/4 of ramus length. Inner apical seta very slender and smooth, about twice as long as ramus. Both principal setae sparsely pinnate at distal end and with breaking plane.

Antennula (Fig. 12B) eight-segmented, unornamented, slender, approximately twice as long as cephalothorax. Very long and slender aesthetasc on fourth segment reaches beyond tip of appendage for more than length of last three segments combined and fused basally with large subapical seta; much smaller and even more slender apical aesthetasc on eighth segment fused basally to two apical setae. Setal formula: 1.8.6.3.2.2.4.7. All setae smooth, except seta on first segment unipinnate; only three setae on eighth segment biarticulating on basal part; no setae with breaking plane. Length ratio of antennular segments, from proximal to distal end and along caudal margin, 1 : 1.4 : 1 : 0.9 : 0.6 : 0.8 : 0.4 : 0.7.

Antenna (Fig. 12C) composed of coxa, basis, two-segmented endopod and one-segmented exopod. Coxa very short, unornamented. Basis about twice as long as wide, unarmed but ornamented with large spinules along inner (anterior) margin. First endopodal segment 1.3 times as long as basis, 2.8 times as long as wide, unornamented and unarmed. Second endopodal segment longest, 1.4 times as long as first and 4.3 times as long as wide, armed laterally with two spines flanking thin seta; apical armature consisting of five geniculate setae, longest one fused basally to additional smaller seta bearing proximal tuft of fine setules; ornamentation consists of few large spinules along anterior proximal surface and two fringes on posterior surface. Exopod one-segmented, half as long as basis and twice as long as wide, unornamented but armed with three setae; innermost (apical) seta 2.8 times as long as exopod, nearly twice as long as middle seta and 1.2 times as long as outermost one; apical seta bipinnate, while other two unipinnate.

Labrum (Fig. 12D) large, trapezoidal, rigidly sclerotized, with relatively wide and slightly convex cutting edge; ornamented with one apical row of small spinules in between two subapical rows of strong spinules, as well as two diagonal rows of hair-like spinules on dorsal (posterior) surface. Two ellipsoid fields of gustatory papillae visible on dorsal surface.

Paragnaths (Fig. 13B) ovoid, fused basally into bilobate labium; each ornamented with apical row of spinules, one spinule on outer margin and longitudinal row of four large curved spinules at middle, close to inner margin, which continues into row of small, hair-like spinules that almost reaches to apical margin.

Mandibula (Fig. 12E) with narrow cutting edge on elongated coxa, armed with numerous small teeth in between one coarse ventral tooth and one dorsal unipinnate seta; ornamentation consists of long row of spinules at base of palp. Palp uniramous, comprising basis and one-segmented endopod. Basis unarmed and

unornamented, 1.8 times as long as wide and 1.3 times as long as endopod. Endopod small and unornamented, about 2.3 times as long as wide; armed apically with four slender smooth setae.

Maxillula (Fig. 13C) with large praecoxa; arthrite rectangular, not movable, unornamented but armed with two smooth setae on anterior surface, two setae on dorsal margin and four apical elements. Coxal endite much shrter than praecoxal arthrite, armed apically with one unipinnate and distally curved seta and two slender smooth setae of subequal length. Basis somewhat shorter than coxal endite, armed with five smooth setae. Endopod very small and fused basally to basis, armed with single smooth apical seta.

Maxilla (Fig. 12F) small, with proximal endite absent; distal endite well developed, highly mobile, armed with one unipinnate spine and two smooth subequal setae. Basis drawn out into long claw, with shorter spiniform seta at its base, ornamented with single pore at base of dorsal seta and row of spinules along concave margin. Endopod represented by minute segment, armed with two smooth, subequal apical setae.

Maxilliped (Fig. 13D) with short syncoxa, twice as long as wide, with few small spinules and single smooth seta near inner distal corner. Basis almost three times as long as wide and 1.3 times as long as syncoxa, unarmed but ornamented with minute spinules along inner margin. Endopod represented by long prehensile claw, ornamented distally with row of spinules along concave side; with thin seta at base.

All swimming legs with three-segmented exopod; endopod of first leg three-segmented (Fig. 12G), endopod of other swimming legs one-segmented (Figs 13E–G). Armature formula of swimming legs as follows (inner/outer element; inner/terminal/outer element):

	Exopod			Endopod		
Segments	1	2	3	1	2 3	
First leg	0/1	0/1	0/2/2	1/0	0/0	1/1/1
Second leg	0/1	1/1	0/2/2	0/1/0	-	-
Third leg	0/1	1/1	0/2/2	1/1/0	-	-
Fourth leg	0/1	1/1	1/2/2	0/1/0	-	-

Intercoxal sclerite of all swimming legs small, with concave distal margin and without surface ornamentation. Praecoxae of all legs unarmed and unornamented. Coxae unarmed but those of first and second legs ornamented with row of spinules on anterior surface; others unornamented. Basis of each leg unornamented, except for few minute spinules at base of inner spine and insertion of endopod on first leg; armed with small outer spine on first and second swimming legs and smooth outer seta on third and fourth legs; first leg with stout spine on inner margin at about 3/5 of its length. All exopodal and endopodal segments ornamented with spinules along outer margin and on outer distal corner; endopod and some exopodal segments with spinules along inner margin as well; inner distal corner of first and second exopodal segments with frilled membrane. All exopodal segments of about same length. First swimming leg (Fig. 12G) with first endopodal segment about three times as long as wide and reaching to 2/3 of second exopodal segment; endopod longer than exopod, reaching beyond distal margin of exopod for length of last endopoal segment. Endopod of second and third swimming legs about as long as first exopodal segment; that of fourth leg somewhat shorter. Apical armature element(s) on first leg geniculate, pinnate on outer (concave) side and either smooth (on endopod) or plumose (on exopod) on inner side. Third exopodal segment of other legs with plumose inner apical seta and heterogeneously ornamented outer apical seta (plumose on inner margin, pinnate on outer; transitional stage between seta and spine). Apical endopodal element of second and fourth legs long, but strong and pinnate, much longer than segment, while that on third leg also spiniform but only slightly longer than segment; inner seta on endopod of third leg slender, plumose and about twice as long as apical element. Inner element on second exopodal segment of second to fourth legs short and spiniform, while all outer exopodal spines strong and bipinnate.

Fifth legs (Fig. 13H) biramous, with each baseoendopod not fused medially together. Baseoendopod with outer basal seta long and smooth, arising from long setophore. Endopodal lobe very broad, only slightly convex, unornamented and armed with two bipinnate elements; outer armature element more robust and 2.1 times as long as inner one. Exopod quadriform, small, about as long as maximum width, unornamented but

armed with four slender smooth setae; length ratio of exopodal setae, from inner to outer side, 1 : 0.6 : 0.3 : 0.7. Longest seta on exopod 0.66 times as long as outer endopodal armature element.

Sixth legs (Fig. 12A) completely fused together, forming simple operculum covering single gonopore, each armed with minute smooth seta.

MALE (ALLOTYPE). Body length 0.472 mm. Habitus (Fig. 14A), ornamentation of prosomites, rostrum, colour and nauplius eye similar to female. Hyaline fringe of all somites smooth. Genital somite twice as wide as long. Single spermatophore (Fig. 14J) longitudinally placed inside fifth pedigerous and genital somites. Anal somite with spinules and sensilla pattern same as in female; anal operculum (Fig. 14B) with posterior row of 11 small spinules.

Caudal rami (Figs 14B–C) slightly shorter and not divergent, with additional dorsal cuticular pore and posterior ventral row of seven spinules; other ornamentation and armature similar to female.

Antennula (Fig. 14D) strongly geniculate, but also long and slender, ten-segmented, with geniculation between seventh and eighth segments, unornamented except for a small dorsal sensillum on first segment. Long aesthetasc on apical acrothek of fifth segment homologous to aesthetasc on fourth segment in female. Smaller aesthetasc on tenth segment fused basally to two apical setae. Armature of first, ninth and tenth segments similar to female. Setal formula: 1.10.6.1.8.1.2.1.4.7. Majority of setae smooth and slender; two setae on fifth segment, one on sixth and one on seventh very short, spiniform and unipinnate; only seta on first segment plumose. Outer (caudal) setae on ninth and tenth segments biarticulating on basal part; no setae with breaking plane.

Antenna, labrum, paragnaths, mandibula, maxillula, maxilla, maxilliped, second swimming leg (Fig. 14F), and fourth swimming leg (Fig. 14H) similar to female.

First swimming leg (Fig. 14E) with inner spine on basis modified, smooth and inflated distally.

Endopod of third swimming leg (Fig. 14G) with inner apical seta significantly shorter than in female, i.e. about as long as apical spine.

Fifth legs (Figs 14I–J) with narrowly fused baseoendopods, each also armed with two elements; inner element similar to female, while outer element smooth, slender and much smaller than in female. Exopod additionally armed with innermost bipinnate seta; second innermost seta (homologous to innermost seta on female exopod) also proportionally longer.

Sixth legs (Fig. 14J) fused basally together and indistinct from somite, each armed with two slender smooth setae; outer seta 1.5 times as long as inner one.

Variability. Only two adult females and one male were collected and studied. Paratype female is slightly smaller (0.531 mm), but no other form of variability was observed. All three specimens were slightly damaged during the collecting and sorting process, with free pedigerous somites deformed and impossible to use for habitus drawings. Some asymmetry observed in the length of the innermost armature element on the fifth leg exopod of the allotype male (Figs 14I–J).

Etymology. The specific name is dedicated to the private environmental consulting agency Ecowise Australia Pty Ltd, who collected the material of this species and partly funded the preparation of this paper. The name is a noun in the genitive singular.

Remarks. With its one-segmented endopod of the second, third and fourth legs, the presence of armature elements on the endopodal lobe of the fifth leg and the armature formula of the swimming legs, *Megastygonitocrella ecowisei* **sp. nov.** is morphologically most similar to the Caucasian *M. ljovuschkini* (Borutzky, 1967) comb. nov. and to the three Australian species described previously from the Pilbara region: *M. trispinosa* (Karanovic, 2006) comb. nov., *M. bispinosa* (Karanovic, 2006) comb. nov. and *M. unispinosa* (Karanovic, 2006) comb. nov. It differs from *M. ljovuschkini* in the plesiomorphic armature of the third exopodal segment of the fourth leg, as well as by having only two armature elements on the endopodal lobe of the female fifth leg (three in *M. ljovuschkini*), but this species is unfortunately incompletely described and many characters in the mouth appendages could not be compared (Borutzky 1967).

The differences between *M. ecowisei* and the three previousy described Australian species are also very small and mostly can be found in the fine details of the ornamentation of the body somites and the armature of

the fifth leg (Karanovic 2006). Additionally, *M. ecowisei* differs from *M. bispinosa* by having only one inner seta on the third expodal segment of the fourth leg (two in the latter species) and a relatively much longer apical spine on the endopod of the second and fourth legs. Although both species have two armature elements on the endopodal lobe of the female fifth leg, they are of a different nature. In *M. ecowisei* they represent the ancestral second and third elements from the outer margin (Table 2, characters 51 & 52), while those in *M. bispinosa* represent the second and fourth elements (characters 51 & 53). The ornamentation of the anal somite is also much more pronounced in *M. bispinosa*. Other small differences can be observed in the proportion of the antennular and antennal segments, structure of the hyaline fringe on the abdominal somites and proportions and ornamentation of the caudal rami.

The ventral ornamentation of the abdominal somites, relative length of the apical endopodal armature element on the second and fourth legs and armature of the endopodal lobe of the fifth leg are some of the most important differences between *M. ecowisei* and *M. unispinosa*. The two species additionally differ by the armature of the maxilliped syncoxa, which in the latter species carries three elements and is probably an atavistic character.

Finally, *M. ecowisei* can be distinguished from *M. trispinosa* by the absence of cuticular windows on the prosomites, reduced ornamentation of the urosomites, proportion of the antennular and antennal segments and endopodal armature elements on the swimming legs, a much shorter copulatory duct of the female genital field and some other small details in the proportion and ornamentation of the mouth appendages. The two species have even been found to live simpatrically in a single bore (i.e. bore PDPIEZ11B above and new material for *M. trispinosa* below), so there is no question about their separate specific status.

Megastygonitocrella pagusregalis **sp. nov.**
(Figs 15 & 16A–E)

Type material. Holotype, adult female dissected on one slide (WAM C37345); Australia, Queensland, Pioneer Valley, bore 12600065, depth 9.57 m, 07 August 2003, leg. P. Hancock, 21°19'37"S 149°00'06"E.

Description. FEMALE (HOLOTYPE). Body length, excluding caudal setae, 0.406 mm. Preserved specimen colourless. Nauplius eye absent. Habitus (Figs 15A–B) cylindrical, slender, without distinct demarcation between prosome and urosome; prosome/urosome ratio 0.9; greatest width at posterior part of cephalothorax, which is only slightly wider than first and second free prosomites. Body length/width ratio about 5.8; cephalothorax only slightly wider than genital double-somite (1.06 times). Free pedigerous somites without pronounced lateral or dorsal expansions. Integument weakly chitinized and without any cuticular windows. Rostrum (Fig. 15A) very small and membranous, not demarcated at base; ornamented with two dorsal sensilla on anterior margin.

Cephalothorax (Figs 15A–B) with completely incorporated first pedigerous somite, almost cylindrical in dorsal view, 1.2 times as long as wide; represents 21% of total body length. Surface of cephalic shield and tergites of three free pedigerous somites ornamented only with several large sensilla. Hyaline fringe of all prosomites narrow and smooth. Fifth pedigerous (first urosomal) somite ornamented only with four dorsal sensilla (two posteriorly and two at midlength); hyaline fringe smooth both dorsally and laterally (Figs 15A–B). Large sclerotized joint (Figs 15A–C) present between fifth pedigerous and genital double somites and visible both ventrally and dorsally.

Genital double-somite (Fig. 15C) approximately 0.8 times as long as wide (ventral view), only slightly wider at posterior part, with suture marking original segmentation clearly visible dorsally and laterally; ornamented with six large sensilla along suture, two posterior dorsal sensilla, four posterior ventral sensilla and one irregular row of relatively large posterior ventral spinules. Hyaline fringe smooth and very narrow. Genital field with single small copulatory pore, sclerotized narrow copulatory duct and two very small, ellipsoid seminal receptacles, posterior part of which not reaching to last third of copulatory duct. Copulatory pore situated at proximal third of double-somite length. Very small genital aperture covered by fused reduced

sixth legs, represents 26% of somite width. Third urosomite (Figs 15B–C) ornamented with six large posterior sensilla (two dorsal and four ventral) and uninterrupted but irregular posterior ventral row of spinules; hyaline fringe smooth. Preanal somite significantly shorter than previous one, more than twice as wide as long and without surface ornamentation. Anal somite (Figs 15C–D) ornamented with pair of large dorsal sensilla, four ventral cuticular pores, interrupted and arched row of spinules ventrally at 1/3 and posterior row of somewhat larger spinules interrupted dorsolaterally and ventrally between caudal rami. Anal operculum convex, not reaching to posterior end of anal somite, represents 49% of somite's width; ornamented near posterior margin with six spinules of about same size as spinules on posterior lateral margin of somite. Anal sinus smooth and widely opened.

Caudal rami (Figs 15B–D) short and conical, shorter than their greatest width (ventral view), slightly divergent, with space between them more than one ramus width; with small diagonal chitinous ridge dorsally and armed with seven setae (three lateral, three apical and one dorsal). Ornamentation consists of two spinules each at base of dorsal and distal lateral setae, one dorsal and one lateral pore and posterior ventral row of five large spinules. Dorsal seta inserted nearly at posterior end and close to inner margin, 2.3 times as long as caudal ramus, triarticulate at its base and smooth. Proximal lateral seta arising somewhat dorsolaterally, 0.7 times as long as dorsal one and 1.7 times as long as distal lateral seta, which arises at 3/4 of ramus length. Inner apical seta very slender and small, smooth, about 0.8 times as long as ramus. Both principal setae inserted slightly more dorsally than terminally, with breaking plane and sparsely pinnate at distal end.

Antennula (Fig. 15E) eight-segmented, but ancestral seventh and eighth segments mostly fused, unusually short and stout, only about as long as cephalothorax, unornamented. Relatively slender aesthetasc on fourth segment reaches beyond tip of appendage for length of more than last four segments combined; much smaller and even more slender apical aesthetasc on eighth segment fused basally to two apical setae. Setal formula: 1.8.6.3.2.2.4.7. All segments, except second and eighth, wider than long. All setae smooth, slender and without breaking plane. Only four setae on eighth segment articulating on basal part. Length ratio of antennular segments, from proximal to distal end and along caudal margin, 1 : 1.6 : 0.7 : 0.8 : 0.6 : 0.6 : 0.3 : 0.8.

Antenna (Fig. 15F) composed of coxa, basis, two-segmented endopod and one-segmented exopod. Coxa very short, unornamented. Basis about 1.3 times as long as wide, unarmed but ornamented with short row of spinules on anterior distal margin. First endopodal segment 1.5 times as long as basis, nearly twice as long as wide, unornamented and unarmed. Second endopodal segment longest, 1.4 times as long as first and 3.1 times as long as wide, armed laterally with two smooth spines flanking thin seta; apical armature consisting of five geniculate setae, longest one fused basally to additional smaller seta bearing proximal tuft of fine setules; ornamentation consists of few spinules along anterior surface and two fringes on posterior surface. Exopod one-segmented, 0.7 times as long as basis and 2.3 times as long as wide, unornamented but armed with three setae; inner (anterior) seta bipinnate, slender, arising apically and 1.5 times as long as other two setae, which are both slightly curved, spiniform and unipinnate at anterior distal part.

Labrum (Fig. 15G) not very large when compared to cephalothorax, trapezoidal, rigidly sclerotized, with relatively broad and convex cutting edge, ornamented with one apical row of smaller spinules in between two subapical rows of strong spinules. Two ellipsoid fields of gustatory papillae visible on dorsal (posterior) surface.

Paragnaths very similar to previous species, but not mounted satisfactorily enough to allow for drawing.

Mandibula (Fig. 15I) very small, with wide cutting edge on relatively short coxa, armed with numerous small teeth in between three coarse ventral teeth and one dorsal unipinnate seta. Palp uniramous, comprising basis and one-segmented endopod. Basis short, unarmed and unornamented, 1.4 times as long as wide and 1.2 times as long as endopod. Endopod small and unornamented, about 1.5 times as long as wide; armed with five slender smooth apical setae.

Maxillula (Fig. 15J) very small compared to body size, with large praecoxa; arthrite rectangular, not movable, unornamented, without smooth setae on anterior surface, armed with three minute setae on dorsal margin and four apical elements (probably three spines and one seta). Coxal endite slightly shorter than

praecoxal arthrite, armed apically with one pinnate and curved and two slender smooth setae, all of about same length. Basis about as long as coxal endite, armed with four smooth setae apically and one subapically. Endopod a minute but distinct segment, armed with smooth apical seta.

Maxilla (Fig. 15K) small, unornamented, with proximal endite on syncoxa absent; distal endite well developed, highly mobile, armed with one pinnate spine and two smooth setae of about same length. Basis drawn out into long claw, with shorter spiniform seta at its base. Endopod represented by minute segment, armed with two smooth and equally long apical setae.

Maxilliped (Fig. 15L) unornamented, with short syncoxa armed with single smooth seta, 1.4 times as long as wide. Basis 2.4 times as long as wide and 1.8 times as long as syncoxa, unarmed. Endopod represented by long curved claw, ornamented distally with row of spinules along concave side; with thin seta at base.

All swimming legs with three-segmented exopod; endopod of first leg three-segmented (Fig. 16A), endopod of other swimming legs one-segmented (Figs 16B–D). Armature formula of swimming legs as follows (inner/outer element; inner/terminal/outer element):

	Exopod			Endopod		
Segments	1	2	3	1	2	3
First leg	0/1	0/1	0/2/2	1/0	0/0	1/1/1
Second leg	0/1	1/1	0/2/2	0/1/0	-	-
Third leg	0/1	1/1	0/2/2	1/1/0	-	-
Fourth leg	0/1	1/1	0/2/2	0/1/0	-	-

Intercoxal sclerite of all swimming legs small, with concave distal margin and without surface ornamentation. Praecoxae short and smooth. Coxa of third leg with two diagonal rows of spinules near outer margin, that of other legs smooth; all coxae unarmed. Basis of each leg ornamented with spinules near outer margin at base of exopod and with smaller ones at base of endopod; first leg additionally with several minute spinules at base of inner spine; armed with small outer spine on first and second swimming legs and smooth outer seta on third and fourth legs; first leg with stout spine on inner margin at about 3/5 of segment length. All exopodal and endopodal segments ornamented with strong spinules along outer margin and on outer distal corner; endopod and some exopodal segments with spinules along inner margin as well; inner distal corner of first and second exopodal segments with frilled membrane. All exopodal segments of about same length. First endopodal segment of first swimming leg (Fig. 16A) about 2.5 times as long as wide and reaching to 2/3 of second exopodal segment; endopod significantly longer than exopod. Endopod of second and third swimming legs about as long as first exopodal segment; that of fourth leg somewhat shorter. Apical armature element(s) on first leg geniculate, pinnate on outer (concave) side and plumose on inner side. Inner apical seta on third exopodal segment of other legs plumose; outer apical seta plumose on inner margin, pinnate on outer (transitional stage between seta and spine). Apical endopodal element of second, third and fourth legs short and spiniform; inner seta on endopod of third leg slender, smooth and about as long as apical element. Inner element on second exopodal segment short and spiniform, while all outer exopodal spines strong and bipinnate.

Fifth leg (Figs 15C, 16E) fused almost completely to somite, represented by two unornamented but armed ventrolateral knobs. Inner knob, representing exopod, armed with three subequal, smooth and slender setae. Outer knob represents outer part of basis and armed with single long unipinnate seta; this seta much longer than any seta on inner knob, reaching to 3/4 of genital double-somite length. Inner part of each baseoendopod absent, fused together into smooth and slightly concave hyaline fringe.

Sixth legs (Fig. 15C) completely fused together, indistinct, forming simple operculum covering single gonopore, without ornamentation or armature.

MALE. Unknown.

Variability. Only one female was collected and studied, and no asymmetric features were observed.

Etymology. The species name is a combination of a Latin noun “pagus” (meaning “district”, “state”) and a Latin possessive adjective “regalis” (meaning “royal”) and is a rough translation of Queensland, the Australian state in which this species was found.

FIGURE 15. *Megastygonitocrella pagusregalis* **gen. et sp. nov.**, holotype female: A—habitus, lateral view; B—habitus, dorsal view; C—urosome, ventral view; D—anal somite and left caudal ramus, lateral view; E—antennula; F—antenna; G—labrum; H—paragnaths; I—mandibula; J—maxillula; K—maxilla; L—maxilliped. Scales = 0.1 mm.

Remarks. As mentioned in the Remarks section for *Megastygonitocrella dec* **sp. nov.**, *M. pagusregalis* **sp. nov.** belongs to a group of very closely related congeners, all with the same segmentation and almost the same armature formula of the swimming legs: *M. ljovuschkini* (Borutzky, 1967) comb. nov., *M. ecowisei* **sp. nov.**, *M. dec* **sp. nov.**, *M. kryptos* **sp. nov.**, *M. trispinosa* (Karanovic, 2006) comb. nov., *M. bispinosa* (Karanovic, 2006) comb. nov. and *M. unispinosa* (Karanovic, 2006) comb. nov. However, it is easily distinguished from all these species by its unusually short antennula and the fifth leg completely fused to the somite. It differs from each species individually by many more characters and we will avoid repeating those differences already stressed in the Remarks sections of other species.

Megastygonitocrella pagusregalis is probably most closely related to the only other species from Queensland, *M. kryptos* **sp. nov.**, and it is unfortunate that the former species is known only from females, while the latter is known only from males, so some characters cannot be compared. Actually, in our preliminary identification of the Queensland material, we entertained for a short time the possibility that they belonged to the same species because of their very similar habitus and swimming legs. However, differences in the ornamentation of the urosomites and anal operculum as well as the shape of the anal operculum and caudal rami all point towards their separate specific status. Also, the fifth leg is not fused to the somite in *M. kryptos,* although the two species have homologous armature elements on this appendage (that of male *M. kryptos* with an additional innermost seta as a normal form of sexual dimorphism in this group of freshwater ameirids). The third exopodal segment of the fouth swimming leg carries one inner seta in *M. kryptos* and none in *M. pagusregalis*, but this character is known to be variable in some species (see, for example, Figs 11E–F).

Megastygonitocrella kryptos **sp. nov.**
(Figs 16F–O)

Type material. Holotype, adult male dissected on one slide (WAM C37346); Australia, Queensland, Pioneer Valley, bore 12600522, depth 15.26 m, 28 June 2003, leg. P. Hancock (jar no. PV37), 21°13'52"S 149°10'11"E.

Other material examined (TOPOTYPES). Two adult males mounted on one slide *in toto* (WAM C37347); Australia, Queensland, Pioneer Valley, bore 12600522, depth 15.26 m, 27 June 2003, leg. P. Hancock (jar no. PV38), 21°13'52"S 149°10'11"E.

Description. MALE (HOLOTYPE). Body length, excluding caudal setae, 0.421 mm. Habitus, ornamentation of prosomites, rostrum, colour and nauplius eye similar to *M. pagusregalis* **sp. nov.** Hyaline fringe of all somites smooth.

Genital somite nearly twice as wide as long. Single large spermatophore (Fig. 16L) placed longitudinally inside fifth pedigerous and genital somites, both of which bear only four large dorsal sensilla each. Third and fourth urosomites (Fig. 16N) each ornamented with only six large posterior sensilla (four ventral and two dorsal); preanal somite without surface ornamentation. Anal somite (Figs 16F & N) ornamented with pair of large dorsal sensilla, two ventral cuticular pores, interrupted but straight row of large spinules at ventral 1/3 and posterior row of large spinules interrupted ventrally between caudal rami. Anal operculum (Fig. 16F) almost straight, not reaching to posterior end of anal somite, represents 42% of somite's width, completely smooth. Anal sinus smooth and widely opened.

Caudal rami (Figs 16F & N) long and very conical, 1.86 times as long as their greatest width (ventral view), slightly divergent, with space between them about one ramus width, without diagonal chitinous ridge dorsally; armed with seven setae (three lateral, three apical and one dorsal). Ornamentation consists of one spinule at base of dorsal seta, posterior ventral row of three small spinules and one dorsal cuticular pore. Dorsal seta inserted close to posterior medial margin, about 1.6 times as long as caudal ramus, triarticulate at its base and smooth. Proximal lateral seta arising somewhat dorsolaterally at midlength, 0.8 times as long as dorsal one and 1.6 times as long as distal lateral seta, which arises at 3/4 of ramus length. Inner apical seta

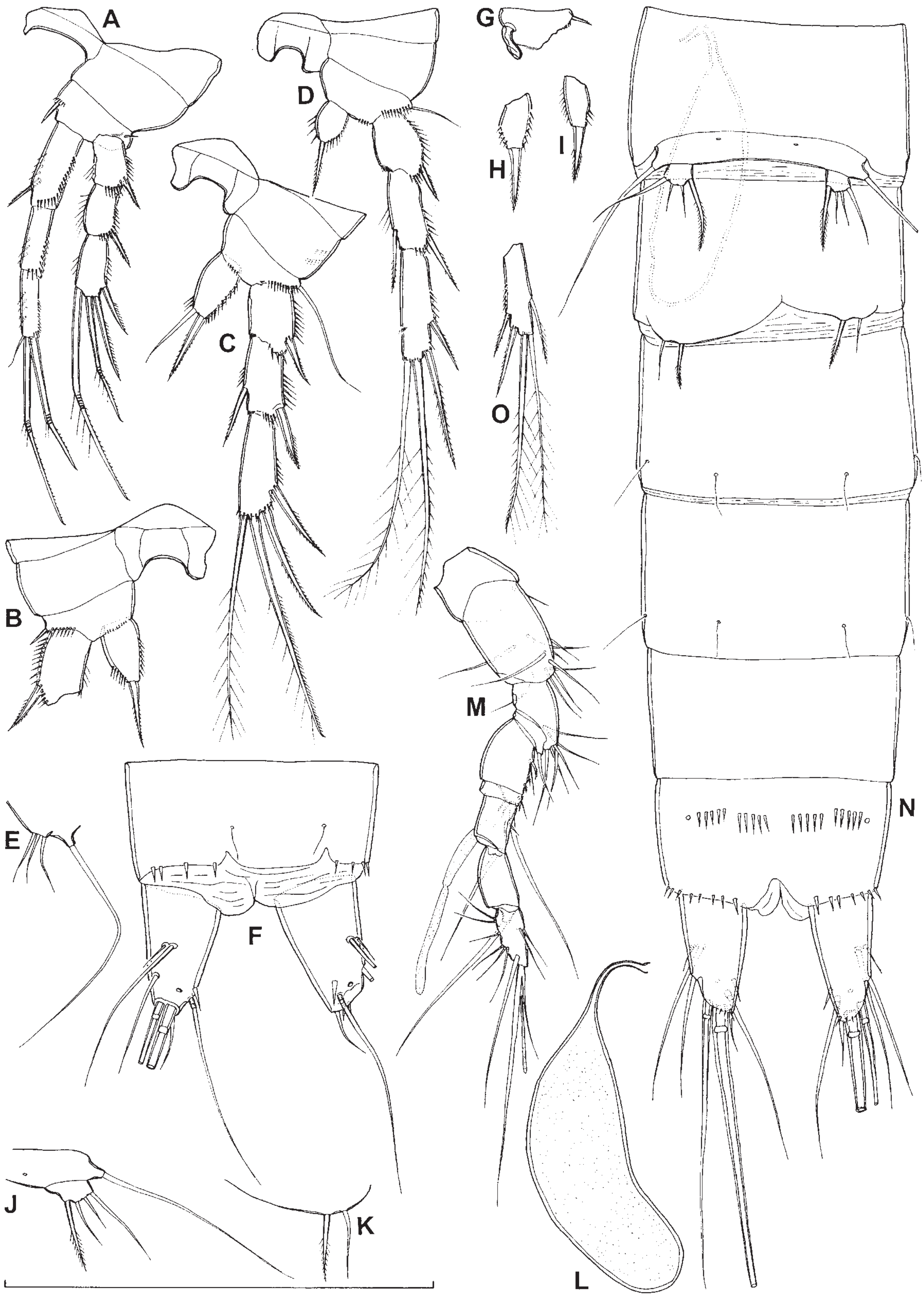

FIGURE 16. *Megastygonitocrella pagusregalis* **gen. et sp. nov.**, A–E, holotype female; *Megastygonitocrella kryptos* **gen. et sp. nov.**, F–M, holotype male; N & O, topotype male (WAM C37347; 0.427 mm): A—first swimming leg; B—second swimming leg without second and third exopodal segments; C—third swimming leg; D—fourth swimming leg; E—left fifth leg; F—anal somite and caudal rami, dorsal view; G—basis of first swimming leg; H—endopod of second swimming leg; I—endopod of fourth swimming leg; J—left fifth leg; K—left sixth leg; L—spermatophore; M—antennula; N—urosome, ventral view; O—third exopodal segment of fourth swimming leg. Scale = 0.1 mm.

slender, small, smooth, about 0.4 times as long as ramus. Both principal setae inserted slightly more dorsally than terminally, smooth and with breaking plane.

Antennula (Fig. 16M) not very long but slender, ten-segmented, but last two segments partly fused, not strongly geniculate, with geniculation between seventh and eighth segments, unornamented. Long aesthetasc on apical acrothek of fifth segment reaching slightly beyond posterior margin of appendage. Setal formula: 1.10.6.1.6.1.2.1.4.7. Majority of setae smooth and slender; three setae on fifth segment, one on sixth and one on seventh very short and spiniform. Outer (caudal) setae on ninth and tenth segments biarticulating on basal part; no setae with breaking plane.

Antenna, labrum, mandibula, maxillula, maxilla, maxilliped, second swimming leg (Fig. 16H) and third swimming leg very similar to *M. pagusregalis* **sp. nov.**

Armature formula of swimming leg as follows (inner/outer element; inner/terminal/outer element):

	Exopod			Endopod		
Segments	1	2	3	1	2	3
First leg	0/1	0/1	0/2/2	1/0	0/0	1/1/1
Second leg	0/1	1/1	0/2/2	0/1/0	-	-
Third leg	0/1	1/1	0/2/2	1/1/0	-	-
Fourth leg	0/1	1/1	1/2/2	0/1/0	-	-

First swimming leg (Fig. 16G) with inner spine on basis modified, smooth, curved outwards apically and very inflated.

Fourth swimming leg (Figs 16I & O) with one inner seta on third exopodal segment and with endopod slightly more elongated than in *M. pagusregalis* **sp. nov.**; all other details of armature, ornamentation and proportions similar to this species.

Fifth legs (Figs 16J & N) with distinct exopod and fused baseoendopods, but distinct from somite. Only ornamentation represented by single cuticular pore on anterior surface of baseoendopod. Exopod small, twice as wide as long, armed with four setae on both sides; innermost seta spiniform and bipinnate, other three smooth and slender; length ratio of exopodal setae 1 : 0.7 : 0.5 : 1.2. Endopodal lobe unarmed. Outer basal seta 2.4 times as long as longest seta on exopod.

Sixth legs (Figs 16K & N) narrowly fused basally together and indistinct from somite, each armed with inner spine and outer seta of about same length.

FEMALE. Unknown.

Variability. Body length of males ranges from 0.421 mm to 0.433 mm (0.427 mm average; n = 3), while no females were collected and studied. One topotype male (WAM C37347) has a somewhat shorter outer seta on the sixth leg (Fig. 16N), as well as the setae on the fifth leg exopod of slightly different proportions. All three males have no ornamentation whatsoever on the anal operculum and have their caudal rami of about the same length.

Etymology. The species name is a Greek adjective "kryptos" (meaning "hidden") and refers to the fact that these three males were preliminarily identified as belonging to *M. pagusregalis* and only careful examination revealed their separate specific status.

Remarks. As mentioned in the Remarks section for the previous species, *Megastygonitocrella kryptos* **sp. nov.** is probably most closely related to the only other representative from Queensland, *M. pagusregalis* **sp. nov.**, but they can be distinguished by a number of characters (see above).

Autapomorphic features of *M. kryptos* include its very narrow anal operculum and elongated, but conical, caudal rami. It is also the only known species in this group where the ancestral middle seta on the male sixth leg is absent, while the other two are present. The structure of the fifth leg resembles that of *M. dec* **sp. nov.**, because it also is not fused to the somite and has a distinct exopod and an endopod that lacks armature. However, a closer examination shows that the ancestral innermost element (Table 2, character 47) of the fifth leg exopod is absent in *M. kryptos* (just like in *M. pagusregalis*), while it is present in *M. dec*. Only two other representatives of *Stygonitocrella s. l.* lack this armature element but both also have lost all the other exopodal

and endopodal armature elements on the fifth leg: *Stygonitocrella orghidani* (Petkovski, 1973) from Cuba and *Reidnitocrella djirgalanica* (Borutzky, 1978) comb. nov. from Kyrgyzstan (see Petkovski 1973; Borutzky 1978; and above). These two species have very little in common with the genus *Megastygonitocrella*, which only shows that the reductions in the fifth leg originated independently a number of times and are not very suitable characters for generic or subgeneric definitions as was done by Suárez-Morales & Iliffe (2005).

***Megastygonitocrella trispinosa* (Karanovic, 2006) comb. nov.**
(Fig. 17)

Synonymy. *Stygonitocrella trispinosa* **sp. nov.** – Karanovic 2006: p. 181, figs 89–93 & 113.

Material examined. One adult male dissected on one slide together with paratype female of *Megastygonitocrella ecowisei* **sp. nov.** (WAM C37354); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Floyd, bore PDPIEZ11B, sample #4110, 10 December 2007, leg. C. Foord & G. Benisson, 20°14'25"S 119°08'40"E.

One adult male dissected on one slide together with one female of *Diacyclops humphreysi humphreysi* Pesce & De Laurentiis, 1996 (WAM C37355); one male and three adult females preserved in 70% ethanol (WAM C37356); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Floyd, bore PDPIEZ04, sample #4109, 10 December 2007, leg. C. Foord & G. Benisson, 20°14'17"S 119°09'21"E.

Three adult males, eight adult females and four copepodids preserved in 70% ethanol (WAM C37357); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Bobby, bore PDRC160, sample #4129, 07 December 2007, leg. C. Foord & G. Benisson, 20°14'39"S 119°07'55"E.

One adult male, 25 adult females and two copepodids preserved in 70% ethanol (WAM C37358); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Bobby, bore PDRC309, sample #4130, 07 December 2007, leg. C. Foord & G. Benisson, 20°14'36"S 119°07'50"E.

Fifteen adult males, 23 adult females and 13 copepodids preserved in 70% ethanol (WAM C37359); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Bobby, bore PDRC310, sample #4131, 07 December 2007, leg. C. Foord & G. Benisson, 20°14'38"S 119°07'51"E.

Fifty-one adult males, 21 adult females and 63 copepodids preserved in 70% ethanol (WAM C37360); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Bobby, bore PDRC468, sample #4133, 07 December 2007, leg. C. Foord & G. Benisson, 20°14'33"S 119°11'18"E.

Thirteen adult males, 39 adult females and 22 copepodids preserved in 70% ethanol (WAM C37361); Australia, Western Australia, Pilbara region, Atlas Iron Mine, bore PDPIEZ02, sample #4134, 07 December 2007, leg. C. Foord & G. Benisson, coordinates not provided.

Twenty-seven adult males, 79 adult females and 41 copepodids preserved in 70% ethanol (WAM C37362); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Bobby, bore PDTEST01, sample #4135, 07 December 2007, leg. C. Foord & G. Benisson, 20°14'37"S 119°07'49"E.

Two adult females and one copepodid preserved in 70% ethanol (WAM C37363); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Lena, bore LRNC015, sample #4138, 03 December 2007, leg. C. Foord & G. Benisson, 20°22'17"S 119°04'22"E.

Two adult males, six females and three copepodids preserved in 70% ethanol (WAM C37364); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Dean, bore PDRC677, sample #4139, 08 December 2007, leg. C. Foord & G. Benisson, 20°14'53"S 119°08'33"E.

Twenty-eight adult males, 22 adult females and 54 copepodids preserved in 70% ethanol (WAM C37365); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Dean, bore PDRC679, sample #4140, 08 February 2008, leg. C. Foord & G. Benisson, 20°14'53"S 119°08'33"E.

Twenty-eight adult males, 45 adult females and 100 copepodids preserved in 70% ethanol (WAM C37366); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Dean, bore PDRC681, sample #4141,

08 December 2007, leg. C. Foord & G. Benisson, 20°14’55”S 119°08’33”E.

Forty-three adult males, 21 adult females and 32 copepodids preserved in 70% ethanol (WAM C37367); Australia, Western Australia, Pilbara region, Atlas Iron Mine, South Limb, bore PDRC090, sample #4155, 11 December 2007, leg. C. Foord & G. Benisson, 20°20’10”S 119°08’35”E.

Nine adult males, 17 adult females and 37 copepodids preserved in 70% ethanol (WAM C37368); Australia, Western Australia, Pilbara region, Atlas Iron Mine, South Limb, bore PDRC092, sample #4156, 11 December 2007, leg. C. Foord & G. Benisson, 20°20’09”S 119°08’37”E.

One adult male and one adult female preserved in 70% ethanol (WAM C37369); Australia, Western Australia, Pilbara region, Atlas Iron Mine, South Limb, bore PDRC188, sample #4159, 02 December 2007, leg. C. Foord & G. Benisson, 20°20’10”S 119°08’34”E.

One adult female preserved in 70% ethanol (WAM C37370); Australia, Western Australia, Pilbara region, Atlas Iron Mine, South Limb, bore PDRC248, sample #4164, 11 December 2007, leg. C. Foord & G. Benisson, 20°20’11”S 119°08’38”E.

Five adult females and three copepodids preserved in 70% ethanol (WAM C37371); Australia, Western Australia, Pilbara region, Atlas Iron Mine, South Limb, bore PDRC254, sample #4166, 03 December 2007, leg. C. Foord & G. Benisson, 20°20’12”S 119°08’41”E.

Seven adult males, 17 adult females and seven copepodids preserved in 70% ethanol (WAM C37372); Australia, Western Australia, Pilbara region, Atlas Iron Mine, South Limb, bore PDRC257, sample #4168, 03 December 2007, leg. C. Foord & G. Benisson, 20°20’10”S 119°08’41”E.

One adult male and two adult females preserved in 70% ethanol (WAM C37373); Australia, Western Australia, Pilbara region, Atlas Iron Mine, South Limb, bore PDRC258, sample #4169, 03 December 2007, leg. C. Foord & G. Benisson, 20°20’11”S 119°08’41”E.

Eleven adult males, six adult females and four copepodids preserved in 70% ethanol (WAM C37374); Australia, Western Australia, Pilbara region, Atlas Iron Mine, South Limb, bore PDRC260, sample #4171, 04 December 2007, leg. C. Foord & G. Benisson, 20°20’08”S 119°08’27”E.

One adult male preserved in 70% ethanol (WAM C37375); Australia, Western Australia, Pilbara region, Atlas Iron Mine, South Limb, bore PDRC261, sample #4172, 04 December 2007, leg. C. Foord & G. Benisson, 20°20’08”S 119°08’28”E.

One copepodid preserved in 70% ethanol (WAM C37376); Australia, Western Australia, Pilbara region, Atlas Iron Mine, South Limb, bore PDRC518, sample #4177, 11 December 2007, leg. C. Foord & G. Benisson, 20°20’11”S 119°08’28”E.

Twenty adult males, 15 adult females and seven copepodids preserved in 70% ethanol (WAM C37377); Australia, Western Australia, Pilbara region, Atlas Iron Mine, South Limb, bore PDPIEZ06, sample #4178, 03 December 2007, leg. C. Foord & G. Benisson, 20°20’09”S 119°08’25”E.

Five adult males, one adult female and one copepodid preserved in 70% ethanol (WAM C37378); Australia, Western Australia, Pilbara region, Atlas Iron Mine, South Limb, bore PDPIEZ08, sample #4179, 02 December 2007, leg. C. Foord & G. Benisson, 20°20’11”S 119°08’32”E.

Six adult males, 41 adult females and 16 copepodids preserved in 70% ethanol (WAM C37379); Australia, Western Australia, Pilbara region, Atlas Iron Mine, South Limb, bore PDPIEZ08, sample #4180, 02 December 2007, leg. C. Foord & G. Benisson, 20°20’11”S 119°08’32”E.

One adult male, two adult females and one copepodid preserved in 70% ethanol (WAM C37380); Australia, Western Australia, Pilbara region, Atlas Iron Mine, South Limb, bore PDTEST02, sample #4182, 03 December 2007, leg. C. Foord & G. Benisson, 20°20’09”S 119°08’31”E.

One adult male and two adult females preserved in 70% ethanol (WAM C37381); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Olivia, bore PDRC162, sample #4196, 09 December 2007, leg. C. Foord & G. Benisson, 20°16’20”S 119°05’44”E.

Two adult females and one copepodid preserved in 70% ethanol (WAM C37382); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Olivia, bore PDRC165, sample #4196, 09 December 2007, leg. C. Foord & G. Benisson, 20°16’19”S 119°06’48”E.

One adult male and one adult female dissected together on one slide (WAM C37383); two adult males, one adult female and one copepodid preserved in 70% ethanol (WAM C37384); Australia, Western Australia, Pilbara region, Balla Balla, bore 75DWPControl1, sample FBN025, 05 December 2007, leg. V. Campagna, 20°46’33”S 117°39’36”E.

Twenty-five adult males, 16 adult females and 10 copepodids preserved in 70% ethanol (WAM C37385); Australia, Western Australia, Pilbara region, Balla Balla, bore 75DWPControl2, sample FBN026, 05 December 2007, leg. V. Campagna, 20°46’40”S 117°39’59”E.

Nineteen adult males, 20 adult females and four copepodids preserved in 70% ethanol (WAM C37386); Australia, Western Australia, Pilbara region, Balla Balla, bore 75DWPControl4, sample FBN027, 05 December 2007, leg. V. Campagna, 20°46’38”S 117°40’26”E.

Four adult males, one adult female and one copepodid preserved in 70% ethanol (WAM C37387); Australia, Western Australia, Pilbara region, Balla Balla, bore 75DWP011, sample FBN028, 05 December 2007, leg. V. Campagna, 20°46’27”S 117°40’42”E.

One adult female preserved in 70% ethanol (WAM C37388); Australia, Western Australia, Pilbara region, Balla Balla, bore 75DWP025, sample FBN030, 05 December 2007, leg. V. Campagna, 20°46’30”S 117°41’52”E.

Nine adult males, 15 adult female and five copepodids preserved in 70% ethanol (WAM C37389); Australia, Western Australia, Pilbara region, Balla Balla, bore BBDW01, sample FBN031, 06 December 2007, leg. V. Campagna, 20°45’50”S 117°46’33”E.

One adult female preserved in 70% ethanol (WAM C37390); Australia, Western Australia, Pilbara region, Balla Balla, bore BBR261, sample FBN033, 06 December 2007, leg. V. Campagna, 20°45’44”S 117°46’13”E.

One adult female almost completely disintegrated and preserved in 70% ethanol (WAM C37391); Australia, Western Australia, Pilbara region, Balla Balla, bore BBMB008, sample FBN034, 04 December 2007, leg. V. Campagna, 20°45’20”S 117°46’43”E.

Two adult males and 10 adult females preserved in 70% ethanol (WAM C37392); Australia, Western Australia, Pilbara region, Balla Balla, bore 76DWP001, sample FBN039, 04 December 2007, leg. V. Campagna, 20°46’24”S 117°44’00”E.

Fifteen adult males, 20 adult females and 19 copepodids preserved in 70% ethanol (WAM C37393); Australia, Western Australia, Pilbara region, Balla Balla, bore 76DWP002, sample FBN040, 04 December 2007, leg. V. Campagna, 20°46’35”S 117°43’48”E.

One adult male, two adult females and three copepodids preserved in 70% ethanol (WAM C37394); Australia, Western Australia, Pilbara region, Balla Balla, bore 99CWP011, sample FBN042, 06 December 2007, leg. V. Campagna, 20°46’22”S 117°47’25”E.

Two adult females preserved in 70% ethanol (WAM C37395); Australia, Western Australia, Pilbara region, Balla Balla, bore BBR071, sample FBN044, 04 December 2007, leg. V. Campagna, 20°45’34”S 117°45’36”E.

One adult female preserved in 70% ethanol (WAM C37396); Australia, Western Australia, Pilbara region, Balla Balla, Black Well impact bore, sample FBN045, 06 December 2007, leg. V. Campagna, 20°46’24”S 117°44’01”E.

One adult male, one adult female and two copepodids preserved in 70% ethanol (WAM C37397); Australia, Western Australia, Pilbara region, Balla Balla, Lauren Bore, sample FBN047, 07 December 2007, leg. V. Campagna, 20°47’28”S 117°40’52”E.

Six adult males, two adult females and five copepodids preserved in 70% ethanol (WAM C37398); Australia, Western Australia, Pilbara region, Balla Balla, Airstrip Bore, sample FBN048, 07 December 2007, leg. V. Campagna, 20°50’16”S 117°48’24”E.

One adult female preserved in 70% ethanol (WAM C37399); Australia, Western Australia, Pilbara region, Balla Balla, bore 76DWP007, sample FBN051, 06 December 2007, leg. V. Campagna, 20°46’46”S 117°43’28”E.

One damaged adult female preserved in 70% ethanol (WAM C37400); Australia, Western Australia, Pilbara region, Balla Balla, bore BBWP04, sample FBN057, 07 December 2007, leg. V. Campagna, 20°45'05"S 117°46'38"E.

One damaged adult male and abdomen of one adult female preserved in 70% ethanol (WAM C37401); Australia, Western Australia, Pilbara region, Balla Balla, bore BBDW01, sample FBN058, 06 December 2007, leg. V. Campagna, 20°45'50"S 117°46'33"E.

One adult male, decomposed and badly damaged, dissected on one slide (WAM C37402); Australia, Western Australia, Pilbara region, Spinifex Ridge, bore SRC057, 08 August 2008, leg. V. Campagna, 20°53'32"S 120°06'35"E.

Three adult males, six adult females and 10 copepodids preserved in 70% ethanol (WAM C37403); Australia, Western Australia, Pilbara region, Spinifex Ridge, bore SRC073, 08 August 2008, leg. V. Campagna, 20°53'17"S 120°06'09"E.

One adult female preserved in 70% ethanol (WAM C37404); Australia, Western Australia, Pilbara region, Spinifex Ridge, bore Box Soak, 08 August 2008, leg. V. Campagna, 20°55'42"S 119°58'32"E.

One adult female dissected on one slide (WAM C37405); three adult males, one adult female and two copepodids preserved in 70% ethanol (WAM C37406); Australia, Western Australia, Pilbara region, Spinifex Ridge, bore SRC057, 14 February 2008, leg. B. Harley & M. Scanlon, 20°53'32"S 120°06'35"E.

One adult female dissected on one slide (WAM C37407); six adult females and two copepodids preserved in 70% ethanol (WAM C37408); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Bobby, bore PDRC309, 06 December 2007, leg. C. Foord & G. Benisson, 20°14'36"S 119°07'50"E.

Four adult males, three adult females and two copepodids preserved in 70% ethanol (WAM C37409); Australia, Western Australia, Pilbara region, Balla Balla, bore BBWP17, sample FBN086, 06 August 2008, leg. V. Campagna, 20°46'23"S 117°46'03"E.

Four adult males and 14 adult females preserved in 70% ethanol (WAM C37410); Australia, Western Australia, Pilbara region, Balla Balla, bore BBWP06, sample FBN087, 05 August 2008, leg. V. Campagna, 20°45'19"S 117°45'48"E.

Two adult males and two adult females preserved in 70% ethanol (WAM C37411); Australia, Western Australia, Pilbara region, Balla Balla, bore BBWP09, sample FBN088, 06 August 2008, leg. V. Campagna, 20°47'14"S 117°48'19"E.

Four adult females preserved in 70% ethanol (WAM C37412); Australia, Western Australia, Pilbara region, Balla Balla, bore BBWP10, sample FBN089, 06 August 2008, leg. V. Campagna, 20°46'56"S 117°48'19"E.

Five adult males, 11 adult females and six copepodids preserved in 70% ethanol (WAM C37413); Australia, Western Australia, Pilbara region, Balla Balla, bore BBWP12, sample FBN091, 06 August 2008, leg. V. Campagna, 20°47'48"S 117°47'10"E.

Two adult males, four adult females and 2 copepodids preserved in 70% ethanol (WAM C37414); Australia, Western Australia, Pilbara region, Balla Balla, bore BBWP16, sample FBN092, 06 August 2008, leg. V. Campagna, 20°48'03"S 117°45'26"E.

One adult female preserved in 70% ethanol (WAM C37415); Australia, Western Australia, Pilbara region, Balla Balla, bore BBWP19, sample FBN094, 06 August 2008, leg. V. Campagna, 20°47'39"S 117°46'45"E.

Eighty-seven adult males, 126 adult females and 149 copepodids preserved in 70% ethanol (WAM C37416); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Bobby, bore PRDC309, 28 April 2007, leg. C. Foord & G. Benisson, 20°14'36"S 119°07'51"E.

Six adult males, 38 adult females and 37 copepodids preserved in 70% ethanol (WAM C37417); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Bobby, bore PRDC317, 28 April 2007, leg. C. Foord & G. Benisson, 20°14'37"S 119°07'49"E.

Nineteen adult males, five adult females and three copepodids preserved in 70% ethanol (WAM C37418); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Bobby, bore PDPIEZ10, 01 May 2007, leg. C. Foord & G. Benisson, 20°14'29"S 119°08'53"E.

Seventeen adult males, 22 adult females and six copepodids preserved in 70% ethanol (WAM C37419); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Bobby, bore PRDC193, 02 May 2007, leg. C. Foord & G. Benisson, 20°14'38"S 119°07'54"E.

Twenty-two adult males, 48 adult females and six copepodids preserved in 70% ethanol (WAM C37420); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Bobby, bore DW, 02 May 2007, leg. C. Foord & G. Benisson, 20°14'37"S 119°07'49"E.

Three adult males, four adult females and one copepodid preserved in 70% ethanol (WAM C37421); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Bobby, bore PRDC175, 09 April 2007, leg. C. Foord & G. Benisson, 20°14'39"S 119°07'46"E.

Two adult males and three copepodids preserved in 70% ethanol (WAM C37422); Australia, Western Australia, Pilbara region, Atlas Iron Mine, South Limb, bore PRDC187, 27 April 2007, leg. C. Foord & G. Benisson, 20°20'13"S 119°08'30"E.

One adult male and one adult female preserved in 70% ethanol (WAM C37423); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Bobby, bore PRDC135, 30 April 2007, leg. C. Foord & G. Benisson, 20°14'40"S 119°07'58"E.

Five adult males and 14 adult females preserved in 70% ethanol (WAM C37424); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Floyd, bore PDPIEZ11B, 01 May 2007, leg. C. Foord & G. Benisson, 20°14'25"S 119°08'40"E.

Two adult males, five adult females and one copepodid preserved in 70% ethanol (WAM C37425); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Bobby, bore PRDC330, 28 April 2007, leg. C. Foord & G. Benisson, 20°14'35"S 119°07'50"E.

One adult female dissected on one slide (WAM C37426); seven adult males, five adult females and seven copepodids preserved in 70% ethanol (WAM C37427); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Alice, bore PRDC232, 02 May 2007, leg. C. Foord & G. Benisson, 20°15'26"S 119°07'13"E.

Three adult males, one adult female and one copepodid preserved in 70% ethanol (WAM C37428); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Olivia, bore PRDC162, 03 May 2007, leg. C. Foord & G. Benisson, 20°16'20"S 119°05'44"E.

Two adult males, four adult females and one copepodid preserved in 70% ethanol (WAM C37429); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Clare, bore PRDC150, 01 May 2007, leg. C. Foord & G. Benisson, 20°14'30"S 119°08'23"E.

One adult male and one adult female preserved in 70% ethanol (WAM C37430); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Clare, bore PRDC340, 01 May 2007, leg. C. Foord & G. Benisson, 20°14'32"S 119°08'24"E.

Eighteen adult males, 12 adult females and four copepodids preserved in 70% ethanol (WAM C37431); Australia, Western Australia, Pilbara region, Atlas Iron Mine, South Limb, bore PRDC095, 04 May 2007, leg. C. Foord & G. Benisson, 20°20'08"S 119°08'30"E.

One adult male and three adult females preserved in 70% ethanol (WAM C37432); Australia, Western Australia, Pilbara region, Atlas Iron Mine, South Limb, bore PRDC257, 26 April 2007, leg. C. Foord & G. Benisson, 20°20'10"S 119°08'41"E.

One adult male and one adult female preserved in 70% ethanol (WAM C37433); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Alice, bore PRDC383, 02 May 2007, leg. C. Foord & G. Benisson, 20°15'24"S 119°07'19"E.

Fourteen adult males, 32 adult females and six copepodids preserved in 70% ethanol (WAM C37434); Australia, Western Australia, Pilbara region, Atlas Iron Mine, South Limb, bore PRDC189, 26 April 2007, leg. C. Foord & G. Benisson, 20°20'12"S 119°08'31"E.

Eleven adult males and 8 adult females preserved in 70% ethanol (WAM C37435); Australia, Western Australia, Pilbara region, Atlas Iron Mine, South Limb, bore PRDC187, 27 April 2007, leg. C. Foord & G. Benisson, 20°20'13"S 119°08'30"E.

Twenty-nine adult males, 53 adult females and 16 copepodids preserved in 70% ethanol (WAM C37436);

Australia, Western Australia, Pilbara region, Atlas Iron Mine, Clare, bore PRDC339, 30 April 2007, leg. C. Foord & G. Benisson, 20°14’31”S 119°08’24”E.

Two adult females preserved in 70% ethanol (WAM C37437); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Glenda, bore PRDC241, 29 April 2007, leg. C. Foord & G. Benisson, 20°14’34”S 119°07’40”E.

Seven adult males, eight adult females and seven copepodids preserved in 70% ethanol (WAM C37438); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Bobby, bore PRDC175, 29 April 2007, leg. C. Foord & G. Benisson, 20°14’39”S 119°07’46”E.

Fourteen adult males, 34 adult females and eight copepodids preserved in 70% ethanol (WAM C37439); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Clare, bore PRDC340, 01 May 2007, leg. C. Foord & G. Benisson, 20°14’32”S 119°08’24”E.

One adult female preserved in 70% ethanol (WAM C37440); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Alice, bore PRDC232, 02 May 2007, leg. C. Foord & G. Benisson, 20°15’26”S 119°07’13”E.

One adult female preserved in 70% ethanol (WAM C37441); Australia, Western Australia, Pilbara region, Atlas Iron Mine, Bobby, bore PRDC193, 02 May 2007, leg. C. Foord & G. Benisson, 20°14’38”S 119°07’54”E.

One adult male, five adult females and five copepodids preserved in 70% ethanol (WAM C37442); Australia, Western Australia, Pilbara region, Atlas Iron Mine, South Limb, bore PRDC203, 26 April 2007, leg. C. Foord & G. Benisson, 20°20’10”S 119°08’38”E.

One adult male and one adult female preserved in 70% ethanol (WAM C37443); Australia, Western Australia, Pilbara region, Quarry 8, bore EXR1622, 23 August 2008, leg. S. Eberhard (sample seLN5211), 22°06’06”S 119°00’10”E.

One adult female dissected on one slide (WAM C37444); Australia, Western Australia, Pilbara region, Quarry 8, bore EXR1619, 02 April 2008, leg. S. Eberhard (sample seLN2345), 22°06’11”S 119°00’14”E.

One adult female preserved in 70% ethanol (WAM C37445); Australia, Western Australia, Pilbara region, Quarry 8, bore EXR1608, 03 April 2008, leg. S. Eberhard (sample seLN2347), 22°05’55”S 118°59’48”E.

Two adult females and one copepodid preserved in 70% ethanol (WAM C37446); Australia, Western Australia, Pilbara region, Yarrie, Salt Bore, 27 April 2008, leg. S. Eberhard (sample seLN2281), 20°36’53”S 120°24’24”E.

One adult female preserved in 70% ethanol (WAM C37447); Australia, Western Australia, Pilbara region (border with Great Sandy Desert), Telfer Gold Mine, bore 54/5.2, date unknown, leg. P. Horwitz, 21°43’41”S 122°12’21”E.

Three adult males and two adult female preserved in 70% ethanol (WAM C37448); Australia, Western Australia, Pilbara region, Balla Balla, Airstrip Bore, samples FBN108 and FBN129, 06 August 2008, leg. V. Campagna, 20°50’15”S 117°54’10”E.

Eight adult males, 19 adult females and five copepodids preserved in 70% ethanol (WAM C37449); Australia, Western Australia, Pilbara region, Balla Balla, bore 75DWP011, sample FBN118, 05 August 2008, leg. V. Campagna, 20°46’27”S 117°40’42”E.

Eight adult males, six adult females and one copepodid preserved in 70% ethanol (WAM C37450); Australia, Western Australia, Pilbara region, Balla Balla, bore 75DWPC4, sample FBN124, 04 August 2008, leg. V. Campagna, 20°46’38”S 117°40’26”E.

Eleven adult males, 36 adult females and three copepodids preserved in 70% ethanol (WAM C37451); Australia, Western Australia, Pilbara region, Balla Balla, bore 75DWP001, sample FBN126, 05 August 2008, leg. V. Campagna, 20°46’24”S 117°44’01”E.

Three adult males and 13 copepodids preserved in 70% ethanol (WAM C37452); Australia, Western Australia, Pilbara region, Balla Balla, bore 76DWP007, sample FBN127, 05 August 2008, leg. V. Campagna, 20°46’46”S 117°43’28”E.

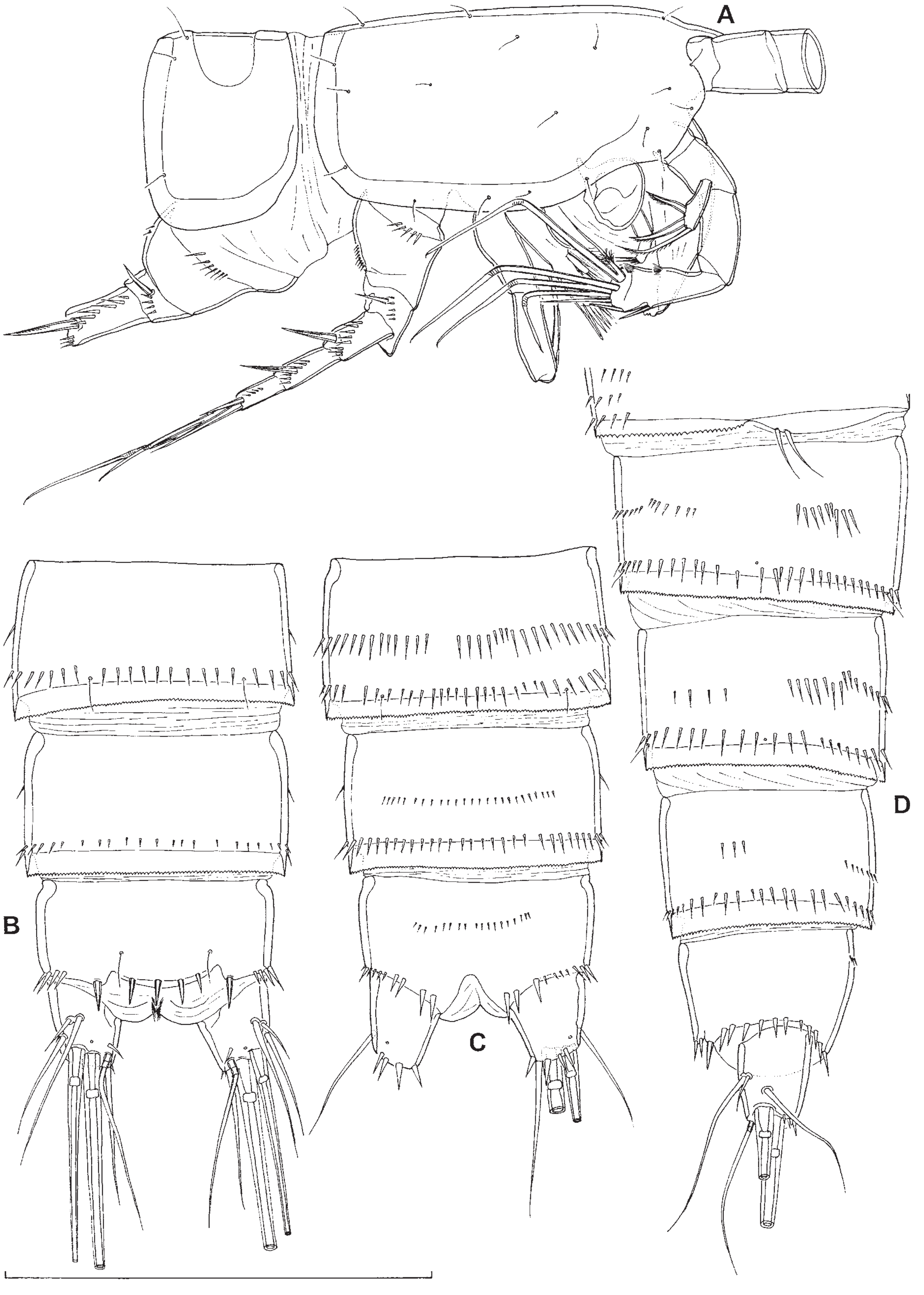

FIGURE 17. *Megastygonitocrella trispinosa* (Karanovic, 2006) comb. nov., male (WAM C37354; 0.445 mm): A—cephalothorax and first free prosomite, lateral view; B—last three urosomites and caudal rami, dorsal view; C—last three urosomites and caudal rami, ventral view; D—abdomen, lateral view. Scale = 0.1 mm.

One adult male and one adult female preserved in 70% ethanol (WAM C37453); Australia, Western Australia, Pilbara region, Balla Balla, bore BBMB008, sample FBN131, 05 August 2008, leg. V. Campagna, 20°45'20"S 117°46'43"E.

Two adult males, six adult females and five copepodids preserved in 70% ethanol (DEC voucher collection); Australia, Western Australia, Pilbara region, De Grey Station, bore GNHSLK1696, 12 June 2003, leg. M. Scanlon & J. Cocking, 20°18'59"S 119°25'35"E.

Twelve adult males, eight adult females and one copepodid preserved in 70% ethanol (DEC voucher collection); Australia, Western Australia, Pilbara region, Carlindi Creek, bore MBSLK388A, 13 June 2003, leg. M. Scanlon & J. Cocking, 20°40'48"S 119°14'43"E.

Three adult females preserved in 70% ethanol (DEC voucher collection); Australia, Western Australia, Pilbara region, West Strelley, bore MBSLK400A, 13 June 2003, leg. M. Scanlon & J. Cocking, 20°36'10"S 119°07'24"E.

One adult male and one adult female dissected on one slide; six adult males and five adult females preserved in 70% ethanol (DEC voucher collection); Australia, Western Australia, Pilbara region, West Strelley, bore MBSLK400B, 13 June 2003, leg. M. Scanlon & J. Cocking, 20°36'10"S 119°07'24"E.

Four adult males, two adult females and one copepodid preserved in 70% ethanol (DEC voucher collection); Australia, Western Australia, Pilbara region, Petermarer Creek, bore GNHSLK1631B, 15 November 2003, leg. M. Scanlon & J. Cocking, 20°23'38"S 118°48'01"E.

One adult female dissected on one slide; two adult males, 10 adult females and one copepodid preserved in 70% ethanol (DEC voucher collection); Australia, Western Australia, Pilbara region, Carlindi Creek, bore MBSLK388A, 15 November 2003, leg. M. Scanlon & J. Cocking, 20°40'48"S 119°14'43"E.

Four adult males, three adult females and three copepodids preserved in 70% ethanol (DEC voucher collection); Australia, Western Australia, Pilbara region, West Strelley, bore MBSLK400B, 15 November 2003, leg. M. Scanlon & J. Cocking, 20°36'10"S 119°07'24"E.

Variability. The most common form of variability in this species, besides small variations in size, is the armature of the endopodal lobe of the female fifth leg. In most specimens it is armed with three spines (although the size of the outermost spine varies), but in some it only carries two spines and sometimes even two spines on one leg and three spines on the opposite appendage. Although variability in characters that are used for the specific name tends to be taken with more caution than any other form, it is probably no more significant than variations in body size or ornamentation patterns. It is interesting to note that the somite ornamentation hardly varies in this species. For example, one male from Atlas Iron Mine has somewhat smaller spinules in the median rows on the preanal and anal somites (Fig. 17C) than those in the allotype, although everything else is exactly the same, including the lateral ornamentation (Fig. 17D), number of spines on the anal operculum (Fig. 17B) and large dorsal cuticular windows on the second and third pedigerous somites (Fig. 17A).

However, in a population from Balla Balla, some specimens were observed with circular lateral cuticular windows on the third and fourth pedigerous somites, in addition to large dorsal windows on the second and third pedigerous somites. In some other bores, zero, a few or all female and male specimens have these lateral windows, but they all clearly have visible dorsal windows. Thus one has to reject the thickness of the cuticulum as a possible explanation for not observing lateral windows in all specimens.

Remarks. *Megastygonitocrella trispinosa* (Karanovic, 2006) comb. nov. was described as *Stygonitocrella trispinosa* from only four different subterranean localities in the Pilbara region (Karanovic 2006), spanning from De Gray River in the north to Fortescue River in the south. However, after the publication of this monograph, stygofauna collecting in the Pilbara region (and other parts of Western Australia) by the Western Australian Department of Environment and Conservation (DEC) and also by many different private environmental consulting agencies doing impact assessment or monitoring studies, mainly for the mining industry, has continued. The senior author was entrusted with the identification of most of the newly collected copepod material and this species turned out to be one of the most common harpacticoids in this region. Here we present new records of this species from an additional 102 samples, taken from over 70 different localities,

which make it the most frequent representative of its genus in Australia and the most frequent member of *Stygnitocrella s. l.* However, its known distribution was not enlarged significantly and the northwesternmost locality (Telfer Gold Mine) is just on the border of the Pilbara region and the Great Sandy Dessert.

All other Australian members of the genus *Megastygonitocrella* **gen. nov.** are short range endemics and are usually collected in very small numbers. In one of the bores *M. trispinosa* was found together with the relatively closely related *M. ecowisei* **sp. nov.** (see above), the former being represented by 20 specimens collected on two occasions (01 May and 10 December 2007), while the latter species had only five, representing the only five ever collected.

While two spines on the endopodal lobe of the female fifth leg, now recognized as variability in some specimens of *M. trispinosa* (see above), is a characteristic of two other Australian species, *M. bispinosa* (Karanovic, 2006) comb. nov. and *M. ecowisei* **sp. nov.**, these three species differ in many other details, including the presence or absence of dorsal cuticular windows on the prosomites, ornamentation of the urosomites, relative length of the first endopodal segment of the first swimming leg, armature of the fourth leg exopod, as well as the shape and size of the transformed spine on the first leg basis in the male. As we explained in the Remarks section for *M. ecowisei*, even the nature of the two fifth leg endopodal spines is different between *M. trispinosa*, *M. ecowisei* and *M. bispinosa*.

Megastygonitocrella unispinosa (Karanovic, 2006) comb. nov.

Synonymy. *Stygonitocrella unispinosa* **sp. nov.** – Karanovic 2006: p. 190, figs 94–97 & 114A–C.

Material examined. One adult female dissected on one slide; one adult male, two adult females and four copepodids preserved in 70% ethanol (DEC voucher collection); Australia, Western Australia, Pilbara region, Fortescue River, Fortescue 4P, bore G70830105P, 19 November 2003, leg. M. Scanlon & J. Cocking, 21°11’57”S 116°03’07”E.

One adult female dissected on one slide; one adult female and two copepodids preserved in 70% ethanol (DEC voucher collection); Australia, Western Australia, Pilbara region, Robe River, near Yarraloola Well, bore PANNASLK24, 19 November 2003, leg. M. Scanlon & J. Cocking, 21°39’50”S 116°08’14”E.

Remarks. This interesting species was described from three different bores in the Robe River aquifer, southwestern Pilbara (Karanovic 2006). Only two additional samples were collected subsequently, one also from the Robe River aquifer and the other from the nearby Fortescue River, which extends its known distribution slightly northwards. However, its range is still less than 50 km in diameter, which suggests that it is a short range endemic. No new variability was recorded in these newly collected specimens.

Megastygonitocrella bispinosa (Karanovic, 2006) comb. nov.

Synonymy. *Stygonitocrella bispinosa* **sp. nov.** – Karanovic 2006: p. 197, figs 98–100 & 114D–F.

Material examined. Two adult males preserved in 70% ethanol (DEC voucher collection); Australia, Western Australia, Pilbara region, Cane River, bore CR11/97, 02 August 2003, leg. M. Scanlon & J. Cocking, 21°43’06”S 115°23’37”E.

Remarks. Originally described from a single bore in the Cane River aquifer (Karanovic 2006), this rare species was collected subsequently only once and less than four kilometres away from the type locality. It is the southernmost representative of the genus *Megastygonitocrella* **gen. nov.** in the Pilbara region. It is interesting to note that no species of *Stygonitocrella s. l.* was collected in the Ashburton River catchment, which is considered to be the southwestern border of this region, or south from the Pilbara region. The two males examined did not have any new variable features.

Discussion

This is the first ever attempt at a phylogenetic analysis of ameirid copepods and here we studied a group of freshwater representatives with a one-segmented endopod of the fourth leg, which all in the past would have been grouped in the genus *Stygonitocrella* Reid, Hunt & Stanley, 2003 (*Stygonitocrella s. l.* in this manuscript), as originally defined by Petkovski (1976). The phylogenetic analysis performed here is a cladistic one, using Rachet Island in the NONA computer program (Goloboff 1999) to search for the most parsimonious tree.

Unfortunately, because of incomplete descriptions of many species, the choice of morphological characters was quite limited, but nevertheless we managed to include in our analysis no less than 57 characters for the 28 species studied. The majority of those (31 characters) are related to the swimming leg armature (see Table 2), as a consequence of a generally unsatisfactory practice of describing new species in this group virtually exclusively on leg characters and with almost no consideration of cephalic appendages, habitus shape or somite ornamentation (Lee & Huys 2002). We decided to study homologous armature elements of the swimming legs and ignore the segmentation patterns (at least in this group), because it has been shown by Rouch (1992) that the two very closely related species of *Psammonitocrella* Huys, 2009, both described from a small creek in Arizona and with many synapomorphic characters (thus undoubtedly sharing a common ancestor), have the endopod of the second and third legs one- or two-segmented. However, their armature formula is quite similar. As pointed out by Lee & Huys (2002), some freshwater ameirid genera have been defined in the past using mostly endopodal segmentation patterns, which can be potentially misleading and the monophyletic status of these groups has not yet been challenged seriously.

The cladistic analysis was performed at the species level, because it is more likely to represent true evolutionary relationships than one based on genera and a few characters (Walker-Smith & Poore 2001). The analysis resulted in only one tree (Fig. 18) with a length of 107 steps, a consistency index (Ci) of 43 and a retention index (Ri) of 63. The values obtained of the Ci and Ri indices indicate a relatively high proportion of convergencies (homoplastic changes). This is obviously a result of the character choices, but it also reflects a general trait within the subterranean freshwater ameirids of an unusual proportion of convergencies within almost any of its groups. That is why at least some of the alleged "symplesiomorphies" in this analysis must be interpreted as a series of homoplastic synapomorphies. Despite the fact that in a classical Hennigian sense symplesiomorphic similarity is not admitted as a criterion to recognize a clade, in order not to blur the picture resulting from the cladistic routine, no further interpretation of homoplastic developments in specific cases has been given here other than accepting the cladogram as it is.

The fact that only one tree was generated and that almost all clades have a support from the zoogeographical distribution patterns already recognized in freshwater copepods (Karanovic 2004a, 2006, 2008) gives us confidence that the results of this cladistic analysis will not change much as more evidence becomes available in a heuristic search for the best, historically correct, cladogram. All clades described as new genera in this paper are supported by what we perceive to be a combination of apomorphic and plesiomorphic characters.

The outgroup taxon in the present analysis, *Biameiropsis barrowensis* Karanovic, 2006 is clearly separated from the rest of the terminal taxa and the ingroup is defined by a number of apomorphic character states, of which most are not even included in the analysis as they would be uninformative. This anchialine ameirid has most morphological characters in their plesiomorphic state and will also be a suitable outgroup for any future cladistic analyses of other freshwater ameirid genera. Among other characters, it has an armed antennal basis, mandibular and maxillular exopod, two maxillar endites, an inner seta on the second endopodal segment of the first leg, three-segmented rami on all swimming legs and a very primitive armature formula of the swimming legs and the fifth leg. Choosing *B. barrowensis* as an outgroup, rather than for example a member of the genus *Nitocrella* Chappuis, 1924, enabled us to easily recognize homologous armature elements on the swimming legs and to code them accordingly.

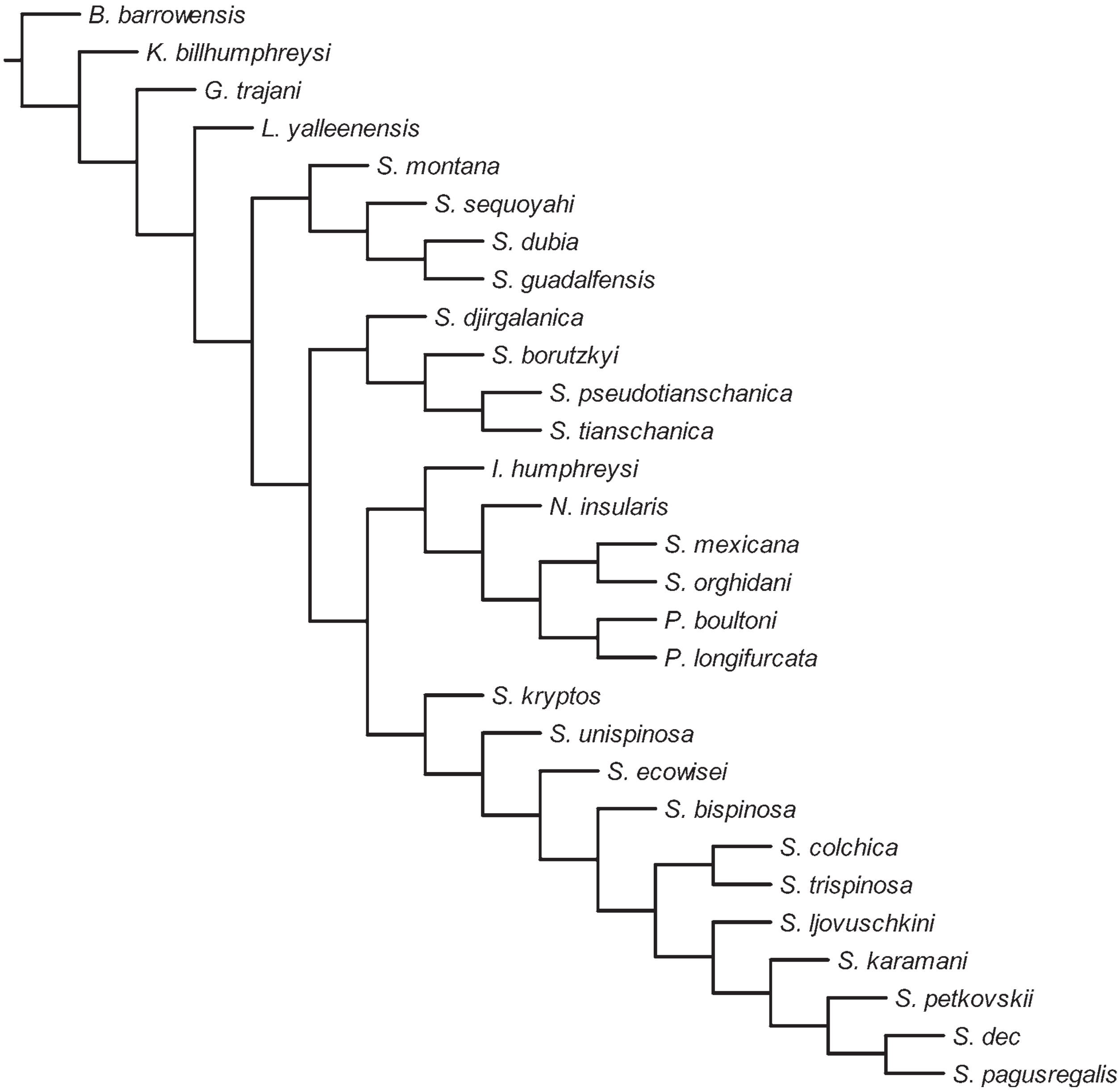

FIGURE 18. Cladogram of the freshwater ameirids with a one-segmented endopod of the fourth leg (*Stygonitocrella s. l.*).

For example, while three armature elements on the ultimate endopodal segment of the third leg can be found in four different species of *Stygonitocrella s. l.*, they cannot be homologous with each other: in *Kimberleynitocrella billhumphreysi* **gen. et sp. nov.** they represent the ancestral outer subapical spine, outer apical seta and distal inner seta, i.e. characters 35, 36 & 38 in Table 2; in *Gordanitocrella trajani* **gen. et sp. nov.** the outer apical seta, distal inner seta and proximal inner seta, i.e. characters 36, 38 & 39; in *Lucionitocrella yalleenensis* **gen. et sp. nov.** the outer apical seta, inner apical seta and proximal inner seta, i.e. characters 36, 37 & 39; and in *Eduardonitocrella mexicana* (Suárez-Morales & Iliffe, 2005) comb. nov. the outer apical seta, inner apical seta and distal inner seta, i.e. characters 36, 37 & 38. A similar comparison can be made for many other leg segments (see Table 2).

In the systematic section we have given the most important characters that define each genus in their respective Remarks sections and we do not want to repeat those here. Also, revised diagnoses are given for the genera *Psammonitocrella*, *Inermipes* Lee & Huys, 2002, *Neonitocrella* Lee & Huys, 2002 and *Stygonitocrella s. str.* The cladogram shows that the three new Australian genera (*Kimberleynitocrella* **gen. nov.**,

Gordanitocrella **gen. nov.** and *Lucionitocrella* **gen. nov.**) are only remotely related to each other and to the rest of the species analysed here, as they exhibit a large number of plesiomorphic characters despite their one-segmented endopod of the fourth leg (note: this segment is reduced to a small unarmed knob in the genus *Kimberleynitocrella*, but nevertheless is present).

Other members of *Stygonitocrella s. l.* are dividied into four large clades, three of which contain species that are very closely related. The first clade consists of four species and because it contains the designated type species of the genus *Stygonitocrella, S. montana* (Noodt, 1965), it is redefined here as *Stygonitocrella s. str*. The main feature that defines this genus is the 1.1.1 armature formula of the ultimate endopodal segment of the second to fourth swimming legs, which cannot be found in any other group studied here. This resulted from the loss of the outer subapical spine on the third leg endopod (character 35 in Table 2) and can only be found in three other species (see the Remarks section for this genus). The genus *Stygonitocrella*, as redefined here, contains only four species: *S. montana* from Argentina; *S. sequoyahi* Reid, Hunt & Stanley, 2003 from the United States of America; and *S. dubia* (Chappuis, 1937) and *S. guadalfensis* Rouch, 1985, both from Spain (see Chappuis 1937; Noodt 1965; Rouch 1985; Reid *et al.* 2003). We also included here *Stygonitocrella orghidani* (Petkovski, 1973) as *incertae sedis* solely on the basis of the endopodal armature of the swimming legs, although it does not cluster at all with this group of freshwater ameirids. Unfortunately, the type material of this species no longer exists (T. Petkovski, pers. comm.) and any further taxonomic decision will have to await a study of newly collected topotypes.

The second clade on the cladogram marks the newly described genus *Reidnitocrella* **gen. nov.**, and, interestingly, all four species come from a relatively small area in central Asia: *R. pseudotianschanica* (Sterba, 1973) comb. nov. from central Afghanistan, while *R. tianschanica* (Borutzky, 1972) comb. nov., *R. djirgalanica* (Borutzky, 1978) comb. nov. and *R. borutzkyi* **sp. nov.** all come from the interstitial of Lake Issyk-Kul in Kyrgyzstan (see Borutzky 1972, 1978; Sterba 1973). Their armature formula of the ultimate endopodal segment of the second to fourth legs is either 2.2.1 or 2.1.1 and the two armature elements on the ultimate endopodal segment of the second leg represent the ancestral outer apical and distal inner setae (characters 26 & 28), which can only be found elsewhere in the completely unrelated genera *Gordanitocrella* **gen. nov.** and *Lucionitocrella* **gen. nov.** Unfortunately, the mouth appendages are practically unknown for all four representatives of *Reidnitocrella*, so many potentially valuable characters could not be included in the cladistic analysis.

The third clade is not very well supported and contains the previously recognized genera *Psammonitocrella*, *Inermipes* and *Neonitocrella*, as well as the above mentioned and very poorly described *S. orghidani* and a species from Mexico that is regarded here as the type species of a new genus *Eduardonitocrella* **gen. nov.**—*E. mexicana*. The latter has a unique armature formula of the ultimate endopodal segment of the second to fourth legs (2.3.3) and can also be distinguished from other genera by a strange combination of apomorphic and plesiomorphic characters (see the Remarks section for *Eduardonitocrella*).

The last and largest clade on the cladogram represents the newly recognized genus *Megastygonitocrella* **gen. nov.**, which contains 11 very closely related species. Seven of those are Australian representatives, found in the Pilbara region in Western Australia and Pioneer Valley in Queensland: *Megastygonitocrella trispinosa* (Karanovic, 2006) comb. nov., *M. unispinosa* (Karanovic, 2006) comb. nov., *M. bispinosa* (Karanovic, 2006) comb. nov., *M. dec* **sp. nov.**, *M. ecowisei* **sp. nov.**, *M. pagusregalis* **sp. nov.** and *M. kryptos* **sp. nov.** (see Karanovic 2006). Two other species were described from Southern Europe, one from Slovenia and the other from the island of Lesbos, Greece: *M. karamani* (Petkovski, 1959) comb. nov. and *M. petkovskii* (Pesce, 1985) comb. nov., respectively (Petkovski 1959; Pesce 1985). The two remaining species were described from the Caucasus (Western Gruzia and the Russian Krasnodarsk Region): *M. colchica* (Borutzky & Michailova-Neikova, 1970) comb. nov. and *M. ljovuschkini* (Borutzky, 1967) comb. nov. (Borutzky 1967; Borutzky & Michailova-Neikova 1970). This distribution pattern would suggest a Tethyan origin of this genus, which is well recognized for many copepod groups found in Western Australia (Karanovic 2004a, 2006). All species lack an inner seta on the second exopodal segment of the first leg, and have only two outer spines on the third

exopodal segment of all swimming legs and no inner armature on the third exopodal segment of the first, second and third legs, in addition to their armature formula of the ultimate endopodal segment of the second to fourth legs (1.2.1 in all, except one species).

Four of the newly erected genera are monospecific, which does not allow the exploration of the robustness of some of the generic characters proposed. However, we expect many new species of this group to be described in the future, as only one region is relatively well explored for stygofauna in Australia (Pilbara), and vast areas of India, Africa, South and North America are still waiting to be sampled. The diversity of freshwater ameirids discovered so far in Australia is nevertheless amazing, both in the number of species and in their characters (Karanovic 2004a, 2006). They are here, unlike in Europe, the most dominant harpacticoid group in subterranean waters, and Karanovic (2006) suggested that differences in family dominance and diversity may reflect a different colonisation history of freshwater subterranean habitats in parts of the former Gondwana and in the Northern Hemisphere. It is interesting to note that representatives of *Stygonitocrella s. l.* do not occur in Australia south of the Tropic of Capricorn and although they are numerous in the Pilbara region they are completely lacking from the neighbouring Murchison region (Karanovic 2004a). Differences between stygofaunas of these two neighbouring regions are astonishing and a "pulsating desert hypothesis" was proposed by Karanovic (2006) as a novel dynamic model that may explain some of them.

Thus, it is exciting to see that some closely related species of *Megastygonitocrella* occur both in the Pilbara region in Western Australia and in tropical Queensland. The importance of looking at small-scale patterns when inferring Gondwanan biogeography was recently demonstrated by Giribet & Edgecombe (2006) for a centipede genus and by Karanovic (2008) for marine interstitial poecilostomatoid and cyclopoid copepods. They found that different parts of Australia have closer affinities to other Gondwana fragments than to each other, which had already been anticipated by Weston & Crisp (1994), who cautioned that assumptions of "monophyly" of large continental blocks such as Australia were unwarranted.

Some very closely related species in this group of freshwater ameirids, and especially among the Australian representatives of the genus *Megastygonitocrella,* with differently reduced fifth legs led us to believe that this character (or this group of characters) is less relevant for reconstructing their phylogenetic relationships. That is why those characters were weighted less in our cladistic analysis. Suárez-Morales & Iliffe (2005) attempted to use the presence/absence of armature elements on the endopodal lobe of this appendage to subdivide the genus *Stygonitocrella.* This simplistic approach would suggest that for example *Megastygonitocrella dec* **sp. nov.** and *M. ecowisei* **sp. nov.** belong to two different genera, although they have identical segmentation and armature of the swimming legs and also very similar cephalic appendages. On the other hand, six new species described in four different genera in this paper all have an unarmed endopodal lobe on the fifth leg. Suárez-Morales & Iliffe's subdivision of the genus is rejected here because it is not taxonomically sound, but also both subgeneric names proved to be junior synonyms of the revised (narrow) genus *Stygonitocrella*. As Wells (2007) pointed out, *Eustygonitocrella* Suárez-Morales & Iliffe, 2005 is obviously an objective synonym of *Stygonitocrella,* since it contains the type species *S. montana*, and must, therefore, be relegated to a junior objective synonym of the nominotypical subgenus (ICZN Article 44.1). For the subgenus *Fiersiella* the authors designated *S. dubia* as "... the representative species ...", without following the rules of the ICZN (Article 67.5), making this genus-group name unavailable. According to the provisions of the Code, type designation must be rigidly constructed by using the term "type species" (or an equivalent term in another language) to avoid ambiguity. Huys (2009) made the subgeneric name available by fixing *S. sequoyahi* as the type species. Our study shows that both *S. dubia* and *S. sequoyahi* belong to the same clade as the type species of *Stygonitocrella*, and therefore, *Fiersiella* Huys, 2009 is deemed here as a junior subjective synonym of the former (see the Remarks section for *Stygonitocrella*).

Below is a key to genera of *Stygonitocrella s. l.*, which can be (with some minor modifications) inserted into the fourth couplet of the family key provided by Boxshall & Halsey (2004). Note that the characters are chosen here for their convenience, not their phylogenetical importance, and one should check the generic diagnoses and Remarks sections for each genus for a full set of distinguishing generic characters.

Key to genera of *Stygonitocrella s. l.*

1	Endopod of fourth leg one-segmented	*Stygonitocrella s. l.*
-	Endopod of fourth leg two- or three-segmented	other Ameiridae
2	Ultimate exopodal segment of first leg with five elements	3
-	This segment with four elements	5
3	Endopod of fourth leg reduced to a small, unarmed knob	*Kimberleynitocrella* **gen. nov.**
-	This segment well developed, armed	4
4	Third exopodal segment of second and third legs with an inner seta	*Gordanitocrella* **gen. nov.**
-	This segment without inner seta	*Eduardonitocrella* **gen. nov.**
5	Third exopodal segment of second leg with two outer spines	6
-	This segment with three outer spines	*Lucionitocrella* **gen. nov.**
6	Endopod of fourth leg reduced to a small, unarmed knob	7
-	This segment well developed, armed with one element	8
7	Second exopodal segment of first leg without outer spine	*Psammonitocrella* Huys, 2009
-	This segment with outer spine	*Neonitocrella* Lee & Huys, 2002
8	Endopod of second leg with single element	*Stygonitocrella* Reid, Hunt & Stanley, 2003
-	This segment with two armature elements	9
9	Lateral seta on endopod of second leg present	*Reidnitocrella* **gen. nov.**
-	This seta absent	9
10	Swimming legs without outer seta on basisInermipes	Lee & Huys, 2002
-	This seta present	*Megastygonitocrella* **gen. nov.**

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